Three new cicada species of the genus *Gudanga* Distant (Insecta: Cicadidae: Cicadettinae: Cicadettini) from Queensland; comparative morphology, songs, behaviour and distributions

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ABSTRACT

Three additional cicada species belonging to the genus Gudanga are described from Queensland. *G. lithgowae* sp. nov. from south east Queeensland, and *G. nowlandi* sp. nov. and *G. emmotti* sp. nov., both from south west Queensland, bringing the total of described Queensland species to five. Detailed comparisons are presented of the morphologies, colourations, distributions and calling songs of the five Queensland Gudanga species. The calling songs are shown to also be characteristic for each of these species. These comprise two distinct song types, those with two echemes per song phrase and those with three echemes per song phrase. The latter type is characteristic of the three new species described in this paper, the specificity of the songs of each of these three species confirmed by detailed statistical analyses. A revised key is presented for the nine known Australian species. ☐ *Cicadettini, cicadas, taxonomy, Gudanga, calling songs, song specificity, acoustic analyses, Queensland, acacias.*

The cicadas belonging to the genus *Gudanga* Distant are distinctive medium-sized insects (15-26 mm body lengths), with black to brown pigmented, semi-opaque to opaque fore wings and usually with orange to crimson pigmentation on at least part of the hind wings. These wing colourations are quite unlike other Australian cicadas. Moulds (1996) reviewed the genus, adding four additional new species (*G. adamsi, G. aurea, G. solata, G. kalgoorliensis*), to the two previously known species (*G. browni* Distant, *G. boulayi* Distant); five of these species are from Western Australia, with one from Queensland (*G. adamsi*). Olive (2007) described an additional species from northern Queensland (*G. pterolongata*). Moulds (2012) has provided, in his comprehensive review of the genera of Australian cicadas, an updated diagnosis of the genus *Gudanga* Distant. Three additional new Queensland species are described here, along with comparisons of the occurrences, distributions, calling songs and taxonomic characteristics of all five Queensland species. A revised key for the identification of the nine Australian *Gudanga* species is also included. The dark fore wing pigmentation ensures that these cicadas are superbly cryptic, in Queensland, within the Mulga (*Acacia* *aneura*), Creekline Mineritchie (*A. cyperophylla*), Brigalow (*A. harpophylla*), Gidyea (*A. cambagei*), or Lancewood (*A. shirleyi*) woodlands in which they most frequently inhabit. This, together with their highly wary nature and fast flight, results in their being visually very inconspicuous cicadas, typically heard far more frequently than seen. Although the songs of the Queensland species are mainly sharp repetitive 'chirping' songs, this work presents detailed aural analyses of their songs which show that each Queensland species has distinctive calling song characteristics.

Documentation of the calling songs is now an important adjunct to the collection of cicadas, proving to be valuable taxonomic tools, and in the field, providing efficient means for identifying known species, and for recognising new species and species complexes, even possible hybridisation (e.g. Ewart, 1998, 2005; Ewart & Popple, 2001; Ewart & Marques, 2008, Marshall *et al*, 2011; Popple & Strange, 2002; Popple, 2003; Popple *et al.*, 2008; Sim□es *et al.*, 2000; Seabra *et al.*, 2006; Sueur, 2002; Sueur & Aubin, 2004).

MATERIALS AND METHODS

Abbreviations. *Institutions and collections.* ANIC, Australian National Insect Collection, Canberra; AE, private collection of A. Ewart, Caloundra; BMNH, the Natural History Museum, London; LWP, private collection of L.W. Popple, Brisbane; JM, private collection of J. Moss, Brisbane; MSM, private collection of M.S. Moulds, Kuranda; QM, Queensland Museum, Brisbane. *Collectors and general.* Hstd, Homestead; NP, National Park; EP, Environmental Park; Rd, Road; Rec, recorded (= aural/electronic song recording); sp, species; spec, specimen; PS, prefix to Queensland Museum photo number; Sta, cattle station; CB, C.J. Burwell; AE, A. Ewart; BJM, B.J. Moulds; MSM, M.S. Moulds; LWP, JM, J. Moss; L.W. Popple. *Morphological.* Measurements (in mm) are given as ranges and means (in parentheses) and include the largest and smallest specimens available. BL, total body length; FWL and FWW, fore wing length and width; HW, head width (across the outer margins of the compound eyes); PW, pronotum width (across the lateral margins, excluding ampliated lateral angles); AW, abdomen width (across the outer edges of the auditory capsules); FWL/WR, fore wing length/width ratio.

Anatomical terminology follows Moulds (2005, 2012) for body and wings, Dugdale (1972) and Moulds (2005, 2012) for genitalia, de Boer (1999) for opercula, and Simmons and Young (1978), Dugdale (1972) and Bennet-Clark (1997) for timbals. The long timbal ribs are referred to sequentially as ribs numbered 1 to 5, with rib 1 being the most posterior (adjacent to timbal plate). The higher classification adopted in this paper follows Moulds (2012).

Song Recordings and Analysis. Although field recordings are generally preferred, a number of earlier song recordings in this project were made of single insects placed within plastic containers, in which small quantities of the relevant vegetation were inserted, as detailed in Ewart & Marques (2008). The primary reasons for use of containers relates to the wary nature, and sometimes erratic singing behaviour of cicadas which can make it difficult to place a microphone in the field environment close enough, for long enough, to directly record meaningful song segments. These container recordings utilised a recording microphone (Sennheiser model K6/ME66) in conjunction with a Sony Walkman cassette recorder WM-D6C model; this recorder responds to near18 kHz, with a linear response to at least 15 kHz. Container recordings provide very low-background noise recordings illustrating subtleties within temporal song characteristics, and can avoid higher frequency filtering which may affect some field recordings. They do, nevertheless, suffer problems with reverberation effects causing some broadening and blurring of pulses, and enhanced splitting of the dominant frequency peaks into discontinuous frequency bands as seen in amplitude and power spectra.

Later recordings were all made in the field, commonly using a parabola (Telinga model with Telinga PRO 5 "Classic" and PRO 6 microphones) allowing direct field recordings, when appropriate direct recordings with a hand held microphone, or by use of a microphone with a collapsible net cage (38cm long by 30cm diameter) hung from convenient vegetation in the field in the habitats of the cicadas in question. Such field recordings are preferred for obtaining long song sequences, detailed analyses of the finer syllable structures of the songs and for frequency analyses using amplitude and/or power spectra. One common problem is background and other interference noise, which can be removed, at least in part, by digital filtering.

The field recordings (AE) were made with a Marantz PMD660 Solid State recorder in conjunction with a Sennheiser model K6/ ME66 microphone, in PCM mode at sampling rate of 48 kHz. Manufacture specifications indicate frequency responses of microphone and recorder to 20.0 kHz (-3.0dB) at 44.1 kHz sampling rate. Other recordings (LWP) utilised a Marantz PMD670 (sampling rate and frequency response as per PMD 660) with a Telinga Pro 6.0 parabolic reflector microphone (frequency response to >18 kHz), or a Tascam DR-07 Compact Flash recorder with an Audio Technica ATR-55 cardioid condenser shotgun microphone (frequency response to 18 kHz). Some additional field recordings were provided by David Marshall, University of Connecticut, using Sony TCD_D8 DAT, Marantz PMD-660 and/or 670 recorders, with Sennheiser ME-62 microphone with Sony 330 parabola. Processing of all recordings was undertaken with Avisoft SAS LabPro software. Two sets of amplitude spectra were run, one with 556-point Fast Fourier Transform with Hamming window on extended song sequences (e.g.20-60 seconds), and a second set on 10 second sequences with 1024-point FFT with Hamming window. Only very minor differences were noted between the data sets, and the latter parameters are used in the plots presented in this paper. Filtering employed the time domain IIR procedure. Amplitude spectra of the *Gudanga* songs exhibit broad band frequency structures, the mean frequency (referred to here as the "dominant frequency") is represented by the mean frequency of the main frequency envelope of each recording as determined by the amplitude and power spectra. The inferred extents of this envelope are shown in the amplitude spectra presented. In addition to dominant frequencies, the amplitude spectra illustrated also list measured sideband frequencies (e.g. Bradbury and Vehrencamp, 1998). These are derived manually from frequency expanded segments of the spectra, using the automatic measuring cursors available in the Avisoft software. Sideband frequencies below about 300 Hz are reproducible in spectra from the same species. Above this frequency, the measured frequencies become progressively less reliable due to uncertainties in their correct identification and significance.

A modified terminology of Ragge and Reynolds (1998) is adapted for the description and analyses of the songs (Ewart, 2005). Although the Ragge-Reynolds terminology was designed for orthopteran insects, there are sufficient similarities in song structures to warrant extending the terminology to the cicada songs described here. The term ***syllable*** is used for discrete but relatively short (≤~2 ms) groups of pulses; where, however, a small but distinct time gap does occur within short grouping of syllables, the term ***diplosyllable*** is used for these syllable pairs. The term ***echeme*** is applied to the first order assemblage of syllables produced during continuous phases of repetitive buckling of the timbal pairs. Where a smaller number of syllables are clearly juxtaposed, these are termed ***macrosyllables***, and are identified as basic echeme components in most songs described here. Time expanded analysis of syllables and macrosyllables allows the resolution of individual pulses and therefore the fundamental frequency carrier waves of the song.

KEY TO SPECIES OF *GUDANGA*

The following key is based on modifications to the original key by Moulds (1996) with the additions by Olive (2007):

1. Abdominal tergites 1-6 black (entirely lacking areas of orange pigmentation)... 9

– Abdominal tergites 1-6 with obvious areas of orange pigmentation 2

2. Hind wing predominantly hyaline, orange at base 3
– Hind wing entirely orange or red basally, remainder fuscous as on forewing 8

3. Orange pigmentation covering basal half of hind wing; remainder hyaline; anal lobe orange with outer half semi-opaque fuscous as on fore wing (northern Qld) . . . .*pterolongata* Olive
– Hind wing without fuscous area on anal lobe 4

4. Hind wing with orange colouration clearly extending beyond anal lobe; weak brown infuscation extending along hind wing margin outside ambient vein. 5
– Hind wing orange colouration almost entirely confined to anal lobe 6

5. Hind wing with orange restricted to proximal half to two-thirds of anal lobe, along 2A vein, and within proximal quarters of anal cell 1 through to radial cells, slightly more extensive on costal cell (eastern-central Qld) . . . . . . *adamsi* Moulds
– Hind wing with extensive orange covering the anal cells through to all but the most distal segments of the cubital to costal cells; very weak orange-brown infuscation on apical cells (south eastern Qld) . . . . *lithgowae* sp.n.

6. Hind wing with orange confined almost entirely to the plaga in anal cell 3 and the area between the plaga and inner margin (southern WA) . . . . . .*kalgoorliensis* Moulds
– Hind wing with orange colouration confined to proximal three-quarters of anal cell 3, proximal half of anal cell 2, extending along 3A and 2A veins; pale orange-brown proximal infuscation on hind wing adjacent to proximal terminations of cubital, medial and costal cells, often extending weakly adjacent to costal and subcostal veins (south western Qld). 7

7. Pygofer secondary basal lobe weakly developed, not markedly swollen and not easily visible except with dissection . .*nowlandi* sp.n.
– Pygofer secondary basal lobe relatively swollen and visible in lateral and dorsal view . . . . *emmotti* sp.n.

8. Pigmentation of hind wing apical cells 1-5 paler than forewing and showing slight orange suffusion (clearly visible when specimen is held approximately 10 cm above a white background); abdomen of male in dorsal view nearly parallel-sided for much of its length (south western WA) . . . . *aurea* Moulds
– Pigmentation of hind wing apical cells 1-5 similar to that of forewing; abdomen of male in dorsal view tapering from base to apex (southern WA) . . . . . . *browni* Distant

9. Base of hind wing crimson; remainder of hind wing usually hyaline but sometimes fuscous (south western WA) . . *boulayi* Distant
– Base of hind wing reddish-orange; remainder of hind wing always fuscous, never hyaline (south western WA) . . . .*solata* Moulds

To facilitate comparison of the new *Gudanga* species with previously described species from Queensland, new drawings (Figs 1–6), and photographs (Plates 1-4) illustrating the morphological features of all five Queensland species are included in this paper.

SYSTEMATICS

Family CICADIDAE Latreille, 1802

Subfamily CICADETTINAE Buckton, 1889

Tribe CICADETTINI Buckton, 1889

Gudanga lithgowae sp. nov.
(Figs 1A-6A, 7, 8B, 10C, 11A, 15A-E, 16D, 18, 19, 20, Plates 1, 4A, Table 1)

Gudanga sp.: Ewart, 1988: 185.
Gudanga adamsi: Ewart, 1998: 62-63, Fig. 8.
Gudanga sp. nr *adamsi*: Popple and Strange, 2002: 28.

Material. HOLOTYPE: ♂, QMT156218, Jct. Auburn-Warrego Rds., Chinchilla, S. Qld, 9-10.i.1994, A.E., 26° 43.64′S 150° 36.76′E (QM).

PARATYPES: Southern Queensland: 1♀, 'Allinga' dam, Chinchilla District, 26° 40′S 150° 38′E, 7.i.1994, G. Lithgow; 4♂, 'Allinga', Lithgow Rd, 26° 39.79′S

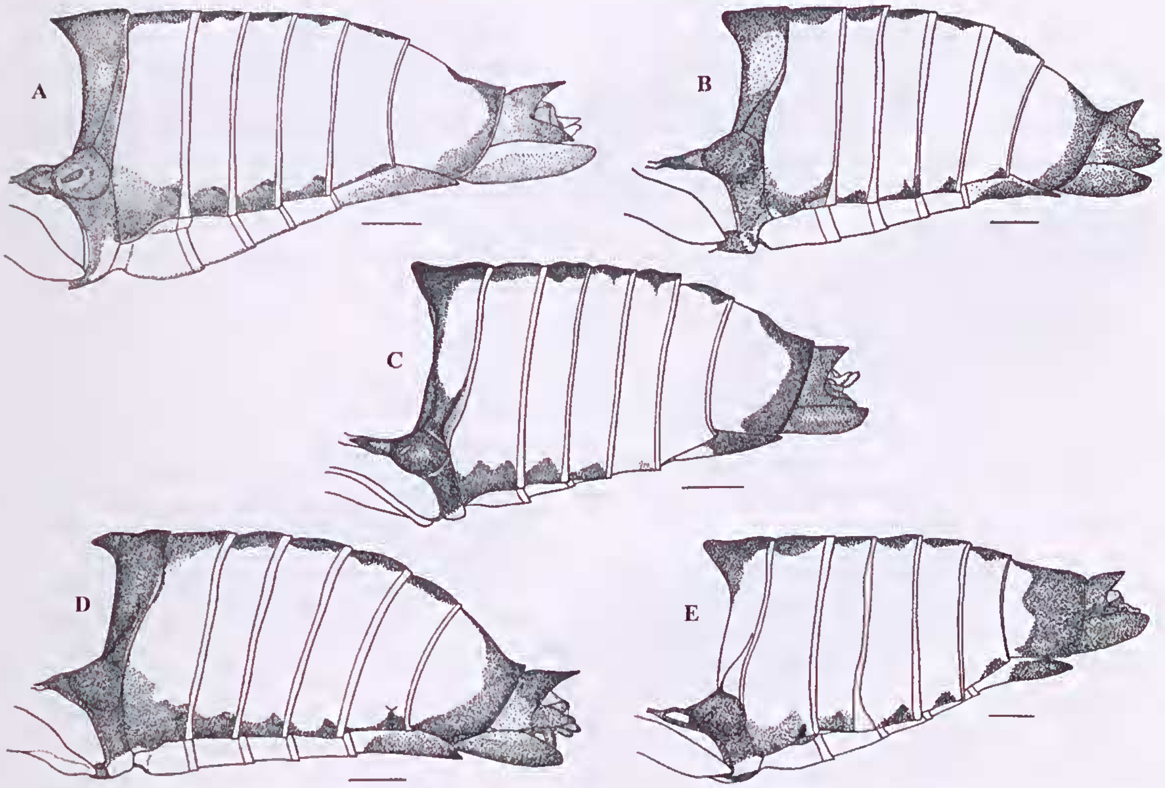


FIG. 1. Lateral abdomen views of males of the five Queensland *Gudanga* species showing the areas of dark pigmentation. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Scale bars are 1 mm.

150° 38.06′E, Chinchilla, 8.i.1994, brigalow, AE; 1♂, 1♀, 'Coo-ee (Stock)Yards', Red Hill Rd, Chinchilla, 26° 38.96′S 150° 38.54′E, 9.i.1994, AE; 14♂, 2♀, Jct. Auburn-Warrego Rds., Chinchilla, 26° 43.64′S 150° 36.76′E, 9-10.i.1994, AE; 2♂, same data, 10.i.1995, AE; 1♂, same data, recorded, 13.xii.1997, AE; 1♂, same data, recorded,4.i.2000, AE; 3♂, 1♀, same data, 22.xii.2001, AE; 1♂, 1♂ (recorded), 'Allinga' Pty, Chinchilla, brigalow, 26° 39.79′S 150° 38.06′E, 9.i.2002, AE (AE). The following paratypes were listed in Moulds (1996) under *G. adamsi*; 1♂, 2♀, "Allinga", Chinchilla, i.1984, 26.xi.1984, 11.xii.1984, G. Lithgow; 3♂, 1♀, "Allinga", Chinchilla, 8.i.1984, J, Moss; 1♀, Allinga Dam, Chinchilla District, 7.i.1994, G. Lithgow; 19♂, 8♀, Auburn Rd, Chinchilla, 8.xii.1987, 9.i.1994, J. Moss (JM). 1♀, Chinchilla, 8.xii.1987, J. Moss, 138-0001; 1♂, Auburn Rd, 2 km W. Chinchilla, 1-3.xii.1999, J. Moss, L. Popple, mv lamp. 139-0002; 3♂, Myall Park, 8 km N. Glenmorgan,27-28.xii.2001, m.v. lamp, L. Popple, R. MacSloy, 139-0003 to 5; 1♂, same data, on minidisc, L.W. Popple, 139-0006; 1♀, 3 km E. Kindon, 10.i.2004, 28° 05′S 150° 47′E, L. Popple, R. MacSloy, 139-0007; 1♂, Southwood N.P. via Moonie, 5-10. xii.2005, 27° 49′51″S 150° 06′14″E, L. Popple, A.E., 139-0009 (LWP). 2♂, AU.QL.SWN, N. edge of Southwood N.P., 27° 48.429′S 150° 05.101′E, 254 m, 31.xii.2008, Hill, Marshall, Moulds, Owen; 1♂, as previously, 1.i.2009; 1♀, as previously, 2.i.2009 (MSM). 1♀, Jct. Auburn-Warrego Rds., Chinchilla, 26° 43.64′S 150° 36.76′E, 9-10.i.1994, AE (QM). 1♂, 1♀, Jct. Auburn-Warrego Rds., Chinchilla, 26° 43.64′S 150° 36.76′E, 9-10.i.1994, AE; (ANIC). 1♂, Jct. Auburn-Warrego Rds., Chinchilla, 26° 43.64′S 150° 36.76′E, 9-10.i.1994, AE; (BMNH). NEW SOUTH WALES: 1♀, *ca*.16 km SE of Boggabilla, 28° 44.673′S 150° 25.050′E, 235 m, 1.i.2005, Hill, Marshall, Moulds (MSM). 1♂, Bundemar Sta., N.E. Trangie, 14.xii.1947, L.J. Chinnick (ANIC).

Description of Male (Figs 1A-6A, Pl. 1A, 4A). *Head*. Compound eyes separated from pronotum along their outer ventral margins; distance between lateral ocelli similar to distance between lateral ocellus and compound eyes. Vertex black, mandibular plate and genae black with narrow sandy-brown narrow ridged margins, covered by mostly short golden pubescence; supra-antennal plate black with pale sandy-brown anterior margins; pale triangular sandy-brown, slightly depressed fascia extending posteriorly from near median ocellus, narrowing towards and extending to pronotal margin. Ocelli rose red. Compound eyes dark brown. Postclypeus black with narrow sandy-brown margin and small dorso-medial pale brown spot. Anteclypeus black; rostrum brown grading to black apically; extends to between mid and hind coxae. Antennae medium brown, darker brown pedicels. Head across outer margins of compound eyes slightly wider than width of pronotum across lateral margins (excepting ampliated lateral angles of pronotal collar).

Thorax. Pronotum predominantly reddish-brown, sometimes dark brown, with irregular black patches adjacent to, and between the paramedian and lateral fissures; sandy-brown central fascia extending posteriorly from near anterior margin, splaying out towards, and fusing with pronotal collar where the sandy-brown core is replaced by black colouration, from which lateral triangular pale sandy-brown extensions run, dorsally to submedially, along the posterior pronotal margin; pronotal collar predominantly black with very narrow pale sandy-brown dorso-lateral posterior margins; narrow pale sandy brown anterior margin; lateral angles of pronotal collar clearly ampliate. Mesonotum predominantly black with the outlines of the black submedial and lateral sigillae largely obscured except for the thin brown line incompletely defining the parapsidal suture, in some specimens extending posteriorly to outer arms of cruciform elevation; lateral mesonotal margins adjacent to wing grooves predominantly pale orange-brown; central dorsal area of cruciform elevation pale to medium brown, remainder, including areas between lateral cruciform elevation arms, black; short, sparse golden pubescence, most pronounced near wing grooves.

Wings. (Fig. 2A). Fore wings commonly black in relatively freshly emerged specimens, evidently fading to semi-opaque, brown colour in older insects and in most dried specimens, always darker immediately adjacent to all veins; conspicuous undulations on the wings between veins; lengths similar to total body length with relatively high length/width ratios (2.6-2.9); costal vein relatively even in width, with minor thickening proximally and with gentle anterior curvature towards node; sclerotised zone along anterior costal vein margin similar in width to costal vein; costal and R+Sc veins fused, but each clearly distinct; nodal line clearly visible in some specimens (as seen in Figs 2C, D); CuA vein not intersecting M vein, but directly intersects arculus of basal cell; 3 distal vein sections of M that form the inner margin of radial cell are of approximately equal length, slightly variable between specimens; medial cell significantly larger than cubital cell; 8 apical cells that are mostly shorter than the adjacent ulner cells; basal membrane orange and opaque; radial cell normally shorter than distance from its apex to wing tip (ratio 0.89-1.04); venation pale to medium brown. Hind wings predominantly hyaline; bright orange opaque plaga covering most of anal cell 3, except for small, apical, well defined, oval-shaped area; approximately one half to two-thirds of anal cell 2 covered by bright orange opaque plaga, the border sharply defined, the plaga extending to and along 2A vein to its distal termination; strong orange infuscation covering the distal hyaline areas of anal cells 2 and 3, and all anal cell 1; deep orange infuscation, almost appearing semi-opaque, fills much of the cubital, medial, radial and costal cells, weakening in intensity in each towards and almost reaching the adjacent apical cells; apical cells with weak orange-brown infuscation also fading towards wing margin; hind wing margin outside ambient vein with weak to distinct brown infuscation, variable between specimens, which just extends into the distal edge of anal cell 2; 6 apical cells; anal lobes clearly broader than cubital cell 1; venation yellow-orange.

Legs. Fore coxae predominantly black with short brown longitudinal fasciae located centrally on lateral and anterior faces; mid and hind coxae predominantly dark brown; fore femora with

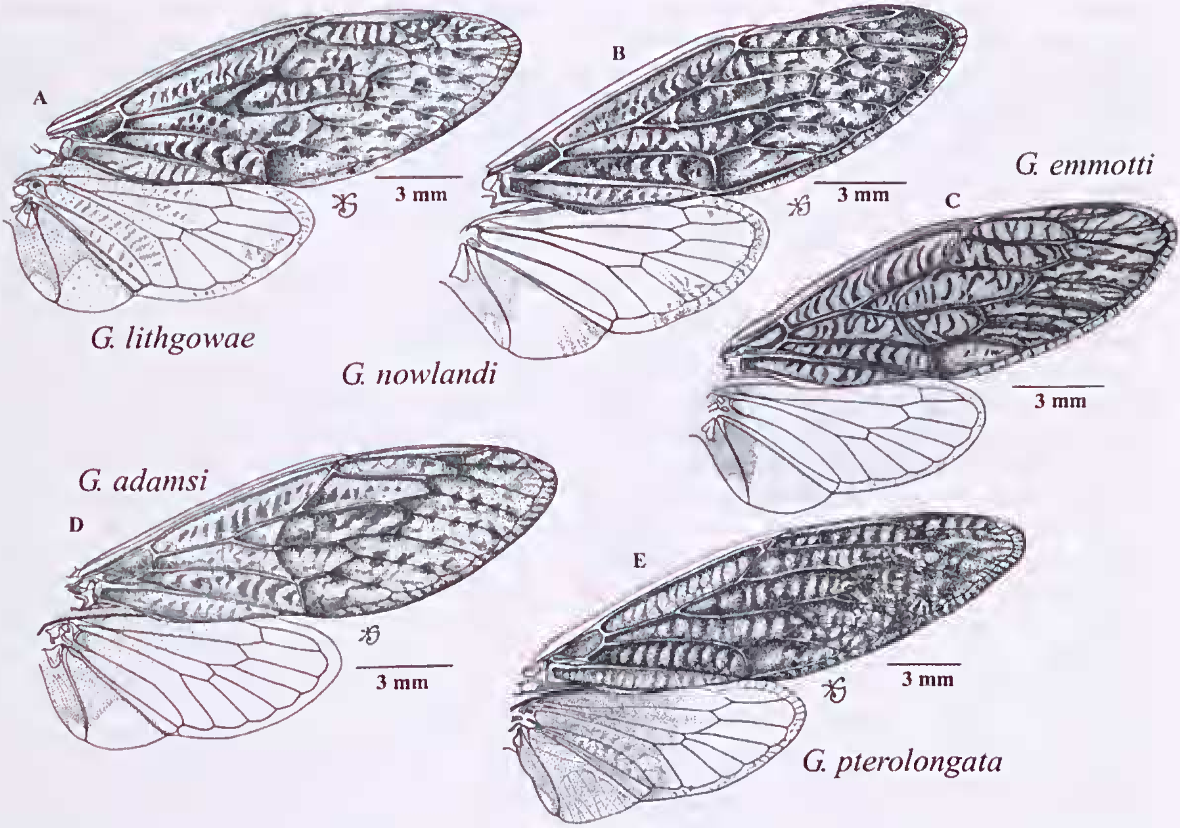


FIG. 2. Fore and hind wings of males of the five Queensland *Gudanga* species, showing the well developed undulations on the fore wings. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Scale bars are 3 mm. Drawings A, B, D, E by Katie Schuler.

alternate longitudinal sandy-brown and dark brown fasciae on each face; mid and hind femora similar but fasciae thinner; trochanters medium to dark brown, being paler brown on hind trochanters; tibiae, tarsi and claws medium brown, pale brown on hind tibiae; tarsi and claws darker apically; 3 black semi-erect spines on fore femora.

Opercula. (Fig. 3A). Relatively elongated roughly parallel to abdomen, although slightly inwardly curved towards abdominal midline in the disto-medial areas of operculum; disto-medial margins rounded; medial margin reaching beyond tympanal cavity margins; distal margin and crest not reaching lateral tympanal cavity margins; inner margins of opercula well separated; opercula developed asymmetrically around meracantha; meracantha spike overlapping timbal plate; broad shallow dome developed across basal and distal areas extending towards crest; domed area medium to dark brown colouration, remaining operculum colouration sandy-brown; opercula usually just reach anterior margin of sternite II in lateral view.

Timbals. (Fig. 4A). Five long ribs, the anterior long rib shortest sometimes barely reaching the adjacent short rib, sometimes clearly overlapping dorsal termination of short rib; long ribs 1 and 2 fused ventrally, long ribs 1 to 3 fused dorsally to basal spur; four well developed short ribs; well developed, elongated dome on timbal plate with shallow grooves oriented along the top of the dome.

Abdomen (Fig. 1A). Width across auditory capsules greater than across lateral pronotal and mesonotal margins, and also across outer margins of compound eyes; in dorsal view, tergites usually gently tapered posteriorly to tergite 6, more strongly curved and tapered along tergites 7 and especially 8, giving a slightly bulbous appearance to abdomen; tergite 2 predominantly black, deep brown on auditory capsules, and with a small orange area developed submedially; black colouration extending anteriorly from tergite 2 to tergite 1, filling area between timbals; tergites 3 to 8 predominantly bright orange, each with a well defined black dorsal area, not extending across intersegmental membranes, and decreasing in size from tergites 3 through to 8; black areas on ventro-lateral margin of each tergite, progressively decreasing in size from tergites 3 to 8, also not extending across intersegmental membranes; the sequence of dorsal black areas give the overall impression of a black fascia extending along the dorsal abdominal surface. Sternites predominantly yellowish sandy-brown; sternite II with small dark median depression; a diffuse brown venter occurs on sternites III to VI, becoming darker in colour and broader on sternites VII and VIII; sternites convex, normally projecting below tergites in lateral view.

Genitalia. (Figs 5A-6A) Pygofer predominantly black including dorsal beak, tending to dark orange colour around anterior margins; prominent upper lobes extending to or beyond anal styles, relatively acutely rounded terminations as seen in lateral view, which dominate the pyofer between the basal lobes and dorsal beak; angle between dorsal margin of upper lobe and its extension to dorsal beak near or slightly less than orthogonal; prominent sharp dorsal beak; well developed basal lobes with rounded apices, visible in lateral view; relatively small but clearly developed, rounded secondary basal lobes; well developed robust claspers, sharply-pointed with hooked terminations; median lobe of uncus conspicuous and duck-bill shaped; aedeagus with theca that is short, simple and tubular which in lateral view has a slanting termination with the posterior rim most prominent; a pair of prominent curved pseudoparameres, sharply pointed apices, much longer than theca and originating closer to theca than its base; theca with short sclerotised ventral support; aedeagal basal plate undulated in lateral view, with broad Y-shape in dorsal view, and functional membraneous 'hinge'.

Description of Female. (Pl. 1B) Similar in general colouration and patterning to male, but with reduction in some specimens in the extent of black pigmentation, sometimes partially replaced by deep brown pigmentation on head, thorax and legs; similar variation occurs in the extent of black or dark brown pigmentation dorsally on abdomen. Slightly larger in size compared to male, with head width across outer margins of compound eyes slightly less than abdominal width across auditory capsules, and both greater than pronotum width across lateral margins. Supra-antennal plate, vertex, mandibular plate, genae and anteclypeus predominantly black to deep brown, with localised brown areas adjacent to pedicels; rostrum brown, black at apex; slightly depressed pale sandy-brown triangular fascia extending from near median ocellus to pronotal margin; ocelli, compound eyes, and postclypeus as in male. Pronotum as in male. Mesonotum with reduced black, and increased brown pigmentation allowing the black short submedial sigillae to be clearly visible, fused anteriorly, rounded posterior terminations; a pair of broadly triangular-shaped lateral sigillae are likewise more clearly visible, with rounded posterior terminations which do not quite reach anterior cruciform elevation arms; areas between and around sigillae medium to dark brown, becoming pale brown around and adjacent to wing grooves; cruciform elevation brown, patchy black areas between anterior and lateral arms. Fore and hind wing pigmentation as in male. Fore coxae and femora similar to male, but with more extensive pale brown fascia; mid and hind coxae predominantly pale brown with localised dark brown patches and thin fasciae anteriorly; fore femora pale brown with dark brown, often irregular fasciae on dorsal and lateral faces; mid and hind femora

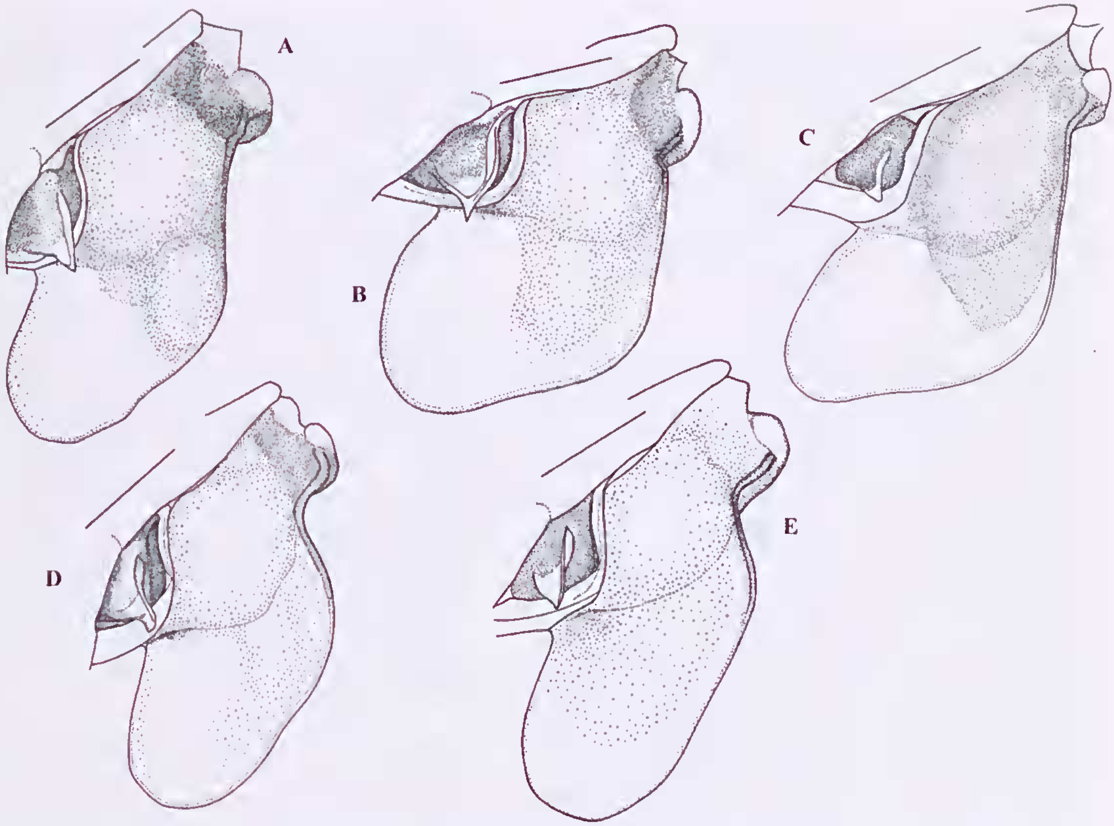


FIG. 3. Left opercula of males of the five Queensland *Gudanga* species. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Scale bars are 1 mm.

pale brown with well developed, narrow dark brown fasciae along anterior and posterior faces; trochanters, tibiae and tarsi medium to pale brown; apices of claws, and spines on fore femora dark brown. Abdomen; tergites 1 and 2 black or dark brown dorsally, tending to brown or light brown ventrally towards the ventro-lateral margins; tergites 3 to 7 with black or deep brown dorsal patches, which on tergite 3 extend submedially along anterior margins; these dorsal black or brown patches extend across intersegmental membranes and decrease sequentially in width towards tergite 7; as viewed dorsally, these dorsal dark patches appear as a prominent longitudinal black fascia running along the abdomen, splaying out strongly anteriorly towards, and within, tergite 2, which in some specimens are much more conspicuous than in the males; dark brown to black patches also occur along ventro-lateral tergite margins of tergites 3 to 7, usually not extending across intersegmental membranes; remaining tergite colouration orange; tergite 8 orange with or without thin discontinuous black patches along posterior margin, a diffuse narrow brown dorsal fascia across tergite, and small dark brown patch on ventro-lateral margin; tergite 9 predominantly orange grading to sandy-brown posteriorly, with a pair of distinct to diffuse (specimen dependent), brown dorso-medial fasciae, each narrowing, darkening, and fusing towards posterior tergite margin; dorsal to dorso-lateral anterior tergite margin with or without darker brown irregular pigmentation; a diffuse spot occurs posterior-laterally. Sternites sandy-brown to medium brown with a median darker brown venter, variable in darker pigmentation intensity between specimens. Ovipositor sheath extends 0.4-0.8 mm beyond apex of tergite 9.

Measurements. N=24♂, 8♀. Ranges and means (in parentheses): *BL*: ♂15.1-18.7 (16.80); ♀ 16.2-20.2 (17.77). *FWL*: ♂ 14.5-17.0 (15.85); ♀ 15.8-19.7 (17.36). *FWW*: ♂ 5.3-6.3 (5.87); ♀ 5.7-7.3 (6.22). *HW*: ♂ 4.5-5.2 (4.84); ♀ 5.0-5.9 (5.19). *PW*: ♂ 4.2-4.8 (4.50); ♀ 4.6-5.5 (4.97). *AW*: ♂ 4.8-5.7 (5.39); ♀ 5.0-6.2 (5.49). *FWL/WR*: ♂ 2.57-2.88 (2.71); ♀ 2.69-2.98 (2.79).

Distribution, Habitat and Behaviour. (Fig. 7) Occurs in inland southeastern and southern Queensland; specific localities include the Chinchilla area; Southwood National Park; Myall Park, 8 km N. of Glenmorgan; near Kindon. Additional southeast Queensland aural records and recordings (LWP) include: 8 and 20 km ENE. of Goondiwindi; Barakula State Forest, N. of Chinchilla; Cameby Downs, between Miles and Chinchilla; 6 km W. of Glenmorgan; Hannaford, between Miles and Moonie; and Wyaga Creek, approximately 60 km NE. Goondiwindi. In N.S.W., specimens are available from ~16 km SE. of Boggabilla and northeast of Trangie. It is a localised species occurring within or associated with Brigalow (*A. harpophylla*) woodland, often where disturbed with dense regrowth. Available records are from mid December to mid January. It is an elusive, cryptic and wary species. The song is a sharp, rapid chirping, described in detail below.

Etymology. Named after Grace Lithgow, (of "Allinga" homestead, Chinchilla) who collected some of the first specimens of the species, and who has also contributed so much to the documentation of the natural history of the Chinchilla region (where the species is locally abundant).

Gudanga nowlandi sp. nov.
(Figs 1B-6B, 7, 9A, 10A, 11 to13, 16A-C, 18, 19, 20, Plates 2, 4B, Tables 1, 3)

Gudanga species B: Ewart and Popple, 2001: 62, 70, Fig. 8C.

Material. TYPES. HOLOTYPE: ♂, QMT156219, 1♂, 'Bulls Gully' lagoon, Adavale, 14.i, 1999, 25° 58.11'S 144° 28.39'E, A.E. (QM).

PARATYPES. SOUTHWESTERN QUEENSLAND: 15♂, 3♀, 'Bulls Gully', Adavale, 13.i.1999, 25° 57.70'S 144° 30.03'E, A.E.; 3♂ recorded, same data; 1♀, same data, 16.i.1999; 1♂, 'Bulls Gully', ~70 km N. Quilpie,,16.iii.1999, 25° 57.74'S 144° 29.19'E, S. & G. Nowland; 1♀, 1.5 km E. 'Bulls Gully', Adavale, 15.i.1999, 25° 57.84'S 144° 29.90'E, A.E.; 2♂, 2.7 km S.W. 'Bulls Gully' Hstd, Adavale, gidyea, 16.ii.1999, 25° 57.91'S 144° 27.88'E, A.E.; 1♂, ~75 km N. Adavale, mulga, 11.xii.2000, 25° 25.07'S 144° 56.97'E, A.E., I.Rattray; 5♂, 1♀, 'Milroy', ~70 kmN. Quilpie, mulga, 11.i.2000, 26° 02.58'S 144° 21.60'E, A.E., I.Rattray; 5♂, 2♀, same data, 8.i.2000; 4♂, same data, 9.i.2000; 1♂, Dam 'Milroy Hstd', ~70 km N. Quilpie, gidyea, 15.i.2000, 26° 02.85'S 144° 20.81'E, A.E., I.R., J.N. (AE). 1♂, Mt. Slowcombe, 3 miles (=5 km) N. of Yaraka, 21.ix.1990, G. Lithgow (listed as paratype of *G. adamsi* in Moulds, 1996) (JM). 5♂, 2♀, Currawinya N.P, 29.x.1998, branches of *Acacia aneura*, Colin Dollery; 2♂, AU.QL.WIN, approx. 63 km SW of Eromanga, 3.ii.2009, 153 m, 27° 2.573'S 142° 53.274'E, K. Hill, D. Marshall; 1♂, AU.QL.DMR, 50 km SE of Windorah, 2.ii.2009, 25° 36.028'S 143° 0.936'E, 140 m, K. Hill, D. Marshall (MSM). ♀, 17.3 km N.E. 'Milroy Hstd', ~90 km N. Quilpie, mulga & turkey bush, 15.i.2000, 25° 56.21'S 144° 22.75'E, A.E., I.Rattray (QM). 1♂, 'Bulls Gully', Adavale, 13.i.1999, 25° 57.70'S 144° 30.03'E, A.E.; 1♀, 17.3 km N.E. 'Milroy Hstd', ~90 km N. Quilpie, mulga & turkey bush, 15.i.2000, 25° 56.21'S 144° 22.75'E, A.E., I.Rattray; (ANIC). 1♂, 'Bulls Gully', Adavale, 13.i.1999, 25° 57.70'S 144° 30.03'E, A.E.; 1♀, 'Milroy', ~70 kmN. Quilpie, mulga, 9.i.2000, 26° 02.58'S 144° 21.60'E, A.E., I.Rattray (BMNH).

Description of Male. (Figs 1B-6B, Pl. 2A, 3B) *Head*. Dark brown compound eyes separated from pronotum along their outer ventral margins; distance between lateral ocelli similar to distance between lateral ocellus and compound eyes; width of head across outer margins of compound eyes greater than across lateral pronotal margins (i.e. excluding ampliated lateral angles of pronotal collar). Supra-antennal plate and vertex black; mandibular plate and genae black with narrow pale brown raised edges, covered by silvery-yellow pubescence, ususally longest on mandibular plate and genae; poorly defined and slightly depressed small pale fascia extending posteriorly from near median ocellus to pronotal margin; small brown patches adjacent to pedicels and along narrow anterior margin of supra-antennal plate, the colour variable from light to dark brown in different specimens. Ocelli pale rose red. Postclypeus shiny black with narrow, pale brown margin; small to very small pale sandy-brown dorso-medial spot. Anteclypeus black; rostrum brown, black apically, extending to beyond the mid coxae, not always quite reaching anterior edges of hind coxae. Antennae brown.

Thorax. Pronotum predominantly black with reddish-brown or deep brown patches between the paramedian fissures, between the paramedian and lateral fissures, and posterio-laterally to lateral fissures; central fascia predominantly black with a small, discontinuous median pale sandy-brown fascia; posterior part of central fascia splays out and merges with the mainly black pronotal collar, except for small sub-medial pale brown patches; the black colour of the pronotal collar continues around the ventro-lateral pronotal margins; anterior pronotal margin pale brown; lateral angles of pronotal collar ampliate. Mesonotum with black submedial and lateral sigillae just visible against the deep brown colouration of the mesonotal areas between and enclosing the sigillae; submedial sigillae relatively short and fused with broad rounded, rounded posterior terminations; lateral sigillae extend posteriorly to anterior arms of cruciform elevation and into area between lateral arms of cruciform elevation; cruciform elevation pale sandy-brown, black along apices of arms; lateral mesonotal margins proximal to wing grooves pale brown; mesonotum with sparse silvery-yellow pubescence, more pronounced adjacent to wing grooves.

Wings. (Fig. 2B) Fore wings semi-opaque, black to brown (apparently browner in worn and dried specimens), relatively darker brown adjacent to all the veins, with conspicuous undulations on the wings between the veins; lengths similar to total body length, with relatively high length/width ratios (2.8-3.1); costal vein very gently curved anteriorly towards node, degree of curvature slightly variable between individuals; sclerotised zone along anterior costal vein margin similar in width to costal vein width; costal and R+Sc veins fused, but each clearly distinct; nodal line clearly visible in some specimens; CuA vein not intersecting M vein, but directly intersects arculus of basal cell; the three distal vein sections of M that form inner margin of radial cell are of unequal length; medial cell larger in size than cubital cell; 8 apical cells that are shorter than adjacent ulnar cells; basal membrane opaque orange; radial cell normally shorter than distance from its apex to wing tip (ratio 0.85-1.00); fore wing venation pale to medium brown. Hind wing predominantly hyaline with variably weak to very weak yellow colouration, always weaker distally; semi-opaque orange plaga covering proximal three-quarters of anal cell 3, the distal margin strongly concavely curved, also covering the proximal third to half of anal cell 2 with obliquely curved or straight margin extending towards vein 2A and further extending adjacent to the vein as narrow colouration to vein termination; the detailed shapes and extents of these areas of orange plaga in anal cells 2 and 3 is variable between individuals; paler orange infuscation variably developed within proximal terminations of cubital cell 1, medial, radial and costal cells, often partially extending weakly adjacent to cubitus, median, subcostal and costal veins; minor weak brown infuscation at distal termination of 2A vein extending very weakly to adjacent margin of anal cell 2; weak but distinct brown infuscation developed along wing margin may be present; 6 apical cells; anal cells 1+2+3 much broader than cubital cell 1+2; hind wing venation orange-brown grading to medium-brown apically.

Legs. Fore coxae predominantly black with short brown longitudinal fasciae located centrally on lateral and anterior faces and three erect black spines; mid and hind coxae dark brown, tending to medium brown distally on hind coxae; fore femora predominantly black with relatively thin brown longitudinal fasciae on each face; mid and hind femora predominantly pale brown with narrow dark brown longitudinal fasciae; fore trochanters, tibiae and tarsi dark brown; mid and hind trochanters, tibiae and tarsi pale brown with diffuse darker brown longitudinal fascia on anterior trochanter faces; claws brown, darker apically.

Opercula. (Fig. 3B) Relatively broad, oriented roughly parallel to abdomen, slightly curved inwards towards abdominal midline in disto-medial area; disto-medial operculum margins broadly rounded; medial margins reaching beyond margin of tympanal cavity while distal margins and crests not reaching lateral

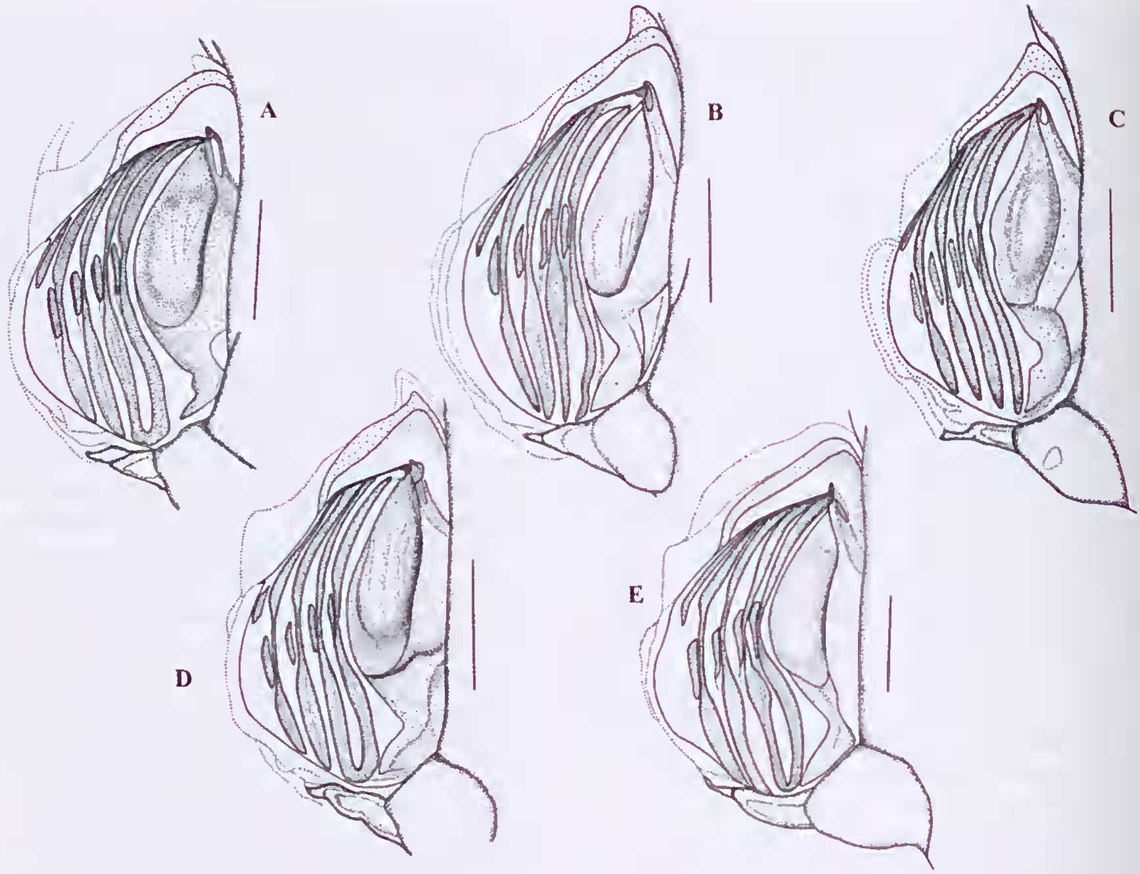


FIG. 4. Timbals of males of the five Queensland *Gudanga* species, with posterior margin at right, dorsal edge at top. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Scale bars are 1 mm.

tympanal cavity margins; inner margins of opercula well separated; opercula developed asymmetrically around meracantha; meracantha spikes overlap operculum plate; broad dome developed across distal and basal areas of opercula extending towards crests; dome areas marked by dark brown colouration, remaining colouration sandy-brown; opercula do not reach anterior margin of sternite II in lateral view.

Timbals. (Fig. 4B) Five long ribs, the anterior long rib shortest, in some specimens overlapping, in other specimens not quite reaching, dorsal termination of adjacent anterior short rib; four well developed short ribs; long ribs 1 to 4 fused dorsally to basal spur, but are not fused ventrally at their terminations; well developed elongated dome on timbal plate with shallow grooves across top of dome.

Abdomen. (Fig. 1B) Width across auditory capsules greater than head width across compound eyes; in dorsal view, tergites gently tapered posteriorly to tergite 6, more strongly curved and tapered along tergites 7 and especially 8, giving a slight bulbous shape to abdomen; tergite 2 black dorsally, the black colouration extending submedially along anterior margin and expanding laterally and ventro-laterally on to, and enclosing the auditory capsules, further extending ventrally along the anterior margin of sternite II; submedial area orange-brown; black dorsal pigmentation of tergite 2 extends anteriorly to tergite 1, filling area between timbals; tergites 3 to 7 predominantly bright orange, each with well defined black dorsal areas not extending across the intersegmental membranes, and decreasing in size from tergite 3 through to 7, with additional dark brown pigmentation along ventro-lateral margins; the black dorsal areas give the overall impression of a black fascia extending dorsally along the abdomen; relatively small, irregular black areas on ventro-lateral margins of tergites 3 to 7, most not extending across intersegmental membranes; tergite 8 orange with broad area of black pigmentation occurring posteriorly and extending to pygofer and dorso-laterally to ventro-laterally around posterior margin. Sternites pale sandy-brown, convex, projecting below tergites in lateral view; abdominal venter with a diffuse and usually weakly developed brown central fascia on sternites II to VI, more strongly developed on sternites VII and VIII; a small black medial depression on sternite II.

Genitalia. (Figs 5B-6B) Pygofer predominantly deep brown to black including dorsal beak; prominent upper lobes extending to anal styles, relatively acutely rounded (although variable) terminations in lateral view which dominate pygofer between basal lobes and dorsal beak; along the dorsal margin of the upper lobe, in some specimens is developed a gentle convex curvature as seen in outline; angle between dorsal margin of upper lobe and it extension to dorsal beak approximately orthogonal; prominent sharp dorsal beak; well developed basal lobes with rounded apices, visible in lateral view; secondary basal lobes present but not strongly developed; robust claspers, sharply pointed, with hooked terminations, roughly parallel; median lobe of uncus conspicuous, somewhat duck-bill shaped; aedeagus with tubular theca which in lateral view has a slanting termination, the posterior rim most prominent; a pair of slightly curved and undulatory pseudoparameres, sharply pointed apices, much longer than theca, originating closer to theca than its base; theca with short sclerotised ventral support; aedeagus basal plate undulated in lateral view, Y-shape in dorsal view, and with functional membraneous 'hinge'.

Female. (Pl. 2B) Similar to male, commonly with subtle reduction in extents of black pigmentation on head, thorax and legs, but generally increased extent of dorsal black pigmentation on abdomen. Head; supra-antennal plate and vertex predominantly black, narrow pale-brown dorso-anterior margin extending to pedicels, even to compound eye; distinct short yellow-brown fascia extending from near median ocellus to pronotal margin; mandibular plate and genae black with pale brown narrow ribbed lateral margins and prominent silver-yellow pubescence; ocelli rose to pale red ; postclypeus predominantly black to deep brown with narrow pale brown margin, partially extending between transverse ridges, distinct pale brown dorso-medial spot; anteclypeus black; rostrum brown, darker brown to black apically, reaching beyond mid-coxae but not always hind coxae; antennae dark brown, pale brown apically. Pronotum predominantly black with reddish-brown or dark brown areas occurring between the lateral and paramedian fissures and on to the lateral margins; central fascia pale brown to yellow-brown, splaying out along posterior pronotal margins; pronotal collar black, thin pale brown posterior margin; remaining pronotal colouration as in male. Mesonotum; similar to male, with submedian sigillae more clearly defined and medium to dark brown pigmentation between sigillae covering mesonotum. Wings as in male, relatively high length/width ratios (2.8-3.1); radial cell shorter than distance from its apex to wing tip (ratios 0.86-0.97). Legs similar to male, but with general reduction of black pigmentation, replaced by dark to medium brown colouration on fore legs; mid and hind legs similar to male. Abdomen, tergites 1 and 2 black or brown dorsally, grading to brown submedially, orange-brown laterally, brown or black on, and enclosing the auditory capsules, but not extending to sternite II; tergites 3 to 8 predominantly bright orange, each with variable dorsal black to brown patches, which are irregular in shape, mostly extending across intersegmental membranes, and showing an

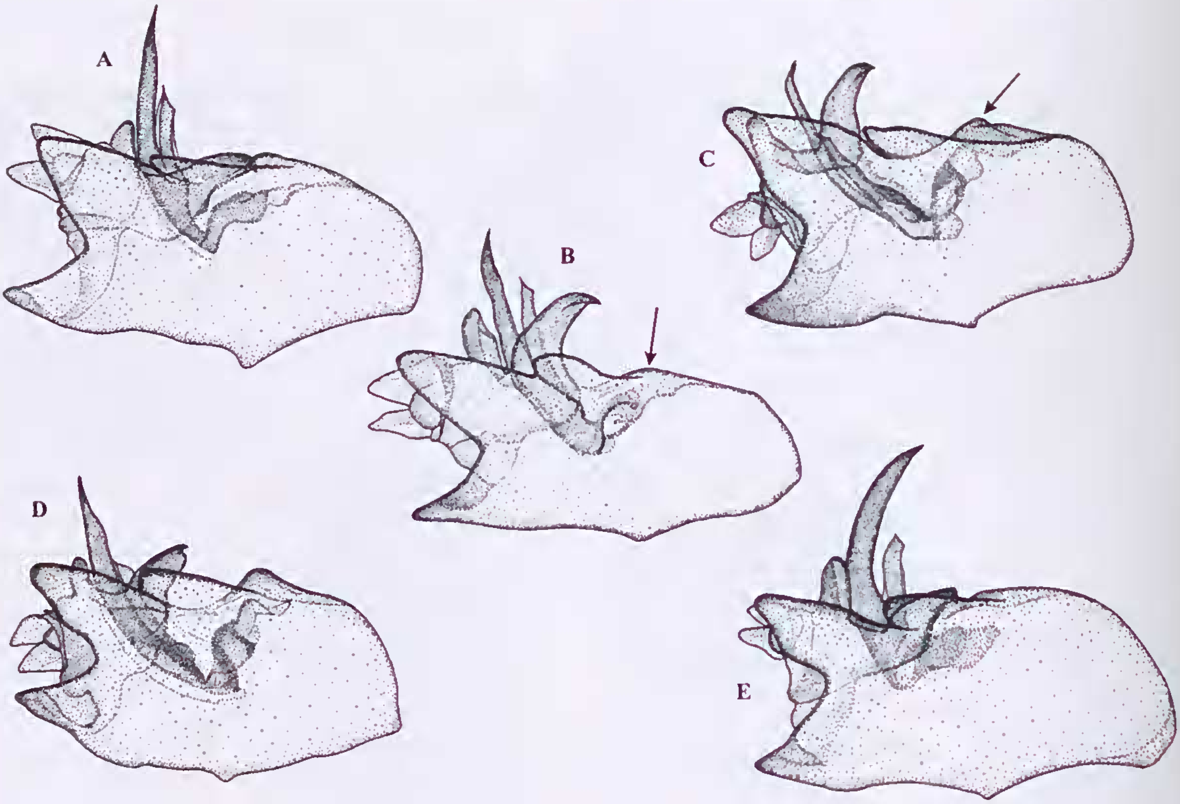


FIG. 5. Pygofer and male genitalia of the five *Gudanga* species illustrated in lateral view. Lengths of pygofers are: 2.3 mm, *G. adamsi;* 2.4 mm, *G. lithgowae;* 2.6 mm, *G. nowlandi;* 2.7 mm *G. emmotti;* 2.5 mm, *G. pterolongata.* Arrows indicate the relatively swollen secondary basal lobes of *G. emmotti* compared to *G. nowlandi*. A, *G. lithgowae;* B, *G. nowlandi;* C, *G. emmotti;* D, *G. adamsi;* E, *G. pterolongata.*

overall narrowing posteriorly towards tergite 8, in addition to a posterior narrowing also evident within each tergite; in dorsal view, these dorsal patches give the appearance of a prominent dark fascia running longitudinally along abdomen, conspicuously splaying out anteriorly towards, and within, tergite 2, more prominent than in the males; deep brown to black diffuse patches also present on ventro-lateral margins of tergites 3 to 8; tergite 9 pale sandy-brown sometimes with an ill-defined broad brown median fascia extending from approximately one-quarter of length of tergite to posterior margin, becoming darker distally, and continuing along submedial posterior margins; in specimens without the median fascia, a pair of submedial, diffuse, slightly curved deep brown to black fasciae occur which extend from anterior tergite margin distally; anterior margin of tergite 9 typically has a deep brown irregular zone, extending and narrowing from the submedial fasciae ventrally towards the ventro-lateral margins; another broad, diffuse zone of brown pigmentation continues partially along ventro-lateral margin; a weak diffuse spot occurs posterior-laterally. Sternites pale yellow to off-white colouration, with or without darker median longitudinal fascia. Ovipositor sheath extends between 0.5-1.3 mm beyond apex of tergite 9.

Measurements. N = 29♂♂, 10♀. Ranges and means (in parentheses): *BL:* ♂ 16.2-20.0 (18.46); ♀ 16.8-20.7 (18.93). *FWL:* ♂ 15.4-18.5 (17.08); ♀ 16.3-20.3 (18.52). *FWW:* ♂ 5.4-6.5 (5.95); ♀ 5.5-

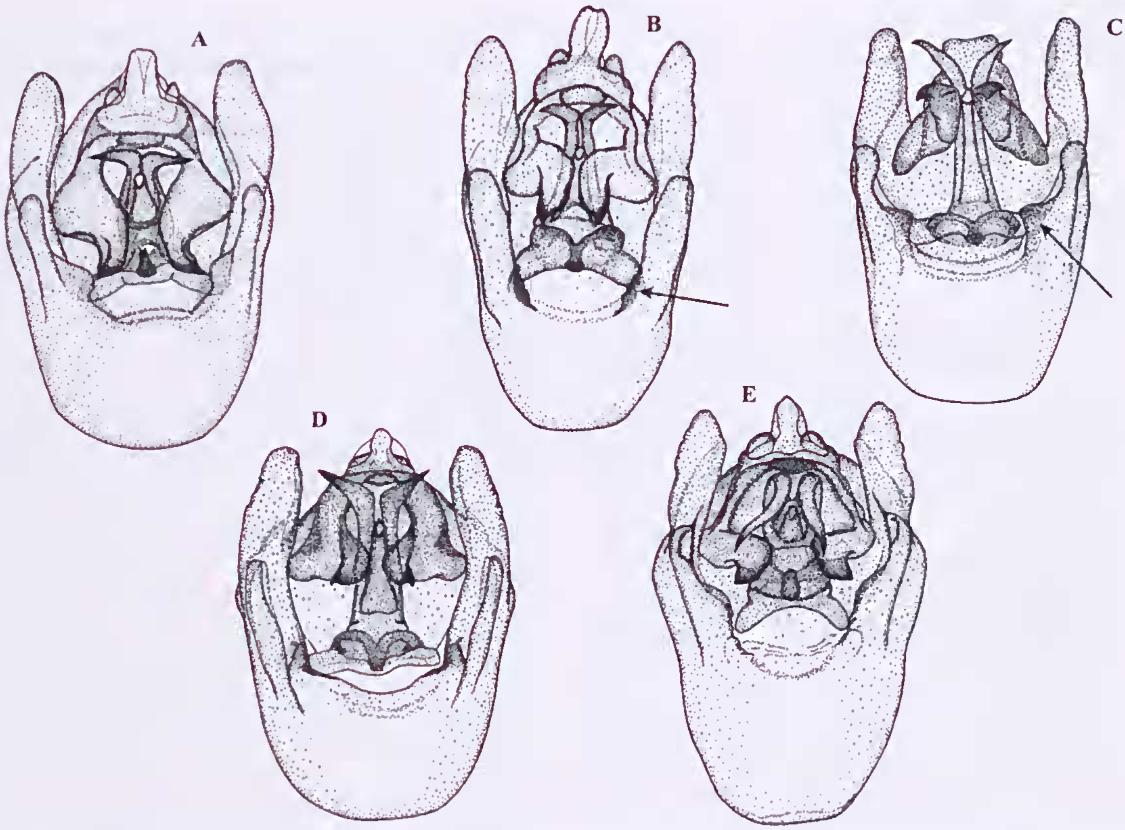


FIG. 6. Pygofer and male genitalia of the five Queensland *Gudanga* species illustrated in ventral view. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Pygofer lengths are listed in Fig. 5 caption. Arrows indicate the relatively swollen secondary basal lobes of *G. emmotti* compared to *G. nowlandi*.

6.8 (6.18). *HW*: ♂ 4.5-5.4 (5.00); ♀ 4.7-5.7 (5.29); *PW*: ♂ 4.2-5.0 (4.68); ♀ 4.5-5.5 (4.94). *AW*: ♂ 5.2-6.3 (5.96); ♀ 5.3-6.1 (5.71). *FWL/WR*: ♂ 2.69-3.02 (2.87); ♀ 2.81-3.14 (3.00).

Distribution, Habitat and Behaviour. (Fig. 7) Known only from the semi-arid region of southwestern Queensland, associated with Mulga (*A. aneura*) woodlands, more rarely Gidyea (*A. cambagei*) woodlands when relatively high populations are present. A localised species, although sometimes locally very common, superbly cryptic, wary and fast flying. Specific localities include: 34 km E Bulloo River crossing at Quilpie (aural records); Mt. Slowcombe, 5 km N of Yaraka; region extending from approximately 70 km N of Quilpie to Adavale, including especially the 'Milroy' and 'Bulls Gully' properties; Boss's Gorge, approximately 75 km N of Adavale, and intervening mulga areas through to Adavale (aural records); the Eulo and Currawinya National Park region; 63 km SW of Eromanga; and 43 km SE of Windorah (near Jundah-Quilpie road junction). The sharp chirping and 'buzzing' song is described below. Available records range from September to March, the optimum months being January to March.

Etymology. Named after J. Nowland, the youngest son of the Nowland families who managed and owned the 'Milroy' and 'Bulls Gully' properties during the time of this study. J. Nowland was active in finding many cicadas, known and undescribed, within the area.

Similar species. *G. nowlandi* is closely similar in morphology and colour patterning to *G. emmotti*, differences being detailed below.

Gudanga emmotti sp. nov.
(1C-6C, 7, 9B, 10B, 11A, 14A-F, 17, 18, 19, 20, Plates 3, 4C, Table 1)

Material. TYPES. HOLOTYPE: ♂, (QMT165702), 200 m W Green Ck, Bald Hills Sta., Tonkoro Rd, SWQ, mulga, 30.i.2009, 24° 05′59.0″S 143° 01′07.2″, K. Hill, A.E. (QM).

PARATYPES. Southwestern Queensland: 1♂, 200 m W Green Ck, Bald Hills Sta., Tonkoro Rd, SWQ, mulga, 30.i.2009, 24° 05′59.0″S 143° 01′07.2″E., K. Hill, AE. (AE). 1♂, 3♀,"Hickleton", SW of Longreach, 27.ii.2004, 23° 59′19″S 143° 03′17″E, A.J. Emmott, P. Kleinschmidt; 5♂, 2♀, Bald Hills Stn nr Noonbah Stn, 18.iii.2003, A.J., F.F. & A.M.M. Emmott, in *Acacia cyperophylla*; 1♀"Noonbah" Stn, SW of Longreach, 18.iii.2003, 24° 04′S 143° 11′E, A.J. Emmott, P. Kleinschmidt; 6♂, 1♀, c.20 km S of Stonehenge, 24° 31′55″S 143° 15′23″E, M.S. & B.J. Moulds; 5♂, 4♀, AU.QL.SSD, 68 km N of Windorah, 1.ii.2009, 24° 56.688′S 142° 51.096′E, 147 m, K. Hill, D. Marshall; 6♂, AU.QL.BHS, Green Ck, 18 km W of Noonbah Hsd., 30.i.2009, 24° 06.071′S 143° 01.054′E, K. Hill, D. Marshall, A. Emmott. (MSM). ♂, 200 m W Green Ck, Bald Hills Sta., Tonkoro Rd, SWQ, mulga, 30.i.2009, 24° 05′59.0″S 143° 01′07.2″E, K.Hill, AE. (BMNH). ♂, 200 m W Green Ck, Bald Hills Sta., Tonkoro Rd, SWQ, mulga, 30.i.2009, 24° 05′59.0″S 143° 01′07.2″E, K. Hill, AE. (ANIC).

Description of Male (1C-6C, Pl. 3A, 4?). *Head.* Dark brown compound eyes separated from pronotum along their outer ventral margins; distance between lateral ocelli similar to distance between lateral ocellus and compound eyes; width of head across outer margins of compound eyes greater than across lateral pronotal margins (i.e. excluding ampliated lateral angles of pronotal collar). Supra-antennal plate and vertex black; mandibular plate and genae black with narrow pale brown raised margins, covered by silvery pubescence, usually longest on mandibular plate and genae; poorly defined and slightly depressed small pale fascia extending posteriorly from near median ocellus to pronotal margin; pale brown margin adjacent to pedicels extending along the dorso-anterior margin of supra-antennal plate, usually continuing in part across vertex to compound eyes. Ocelli pale red. Postclypeus shiny black with narrow, pale brown margin; small to very small diffuse pale sandy-brown dorso-medial spot. Anteclypeus black; rostrum brown, black apically, extending beyond mid coxae, usually just reaching anterior margin of hind coxae. Antennae brown.

Thorax. Pronotum predominantly black with conspicuous reddish-brown, less often deep brown areas between the paramedian fissures, between the paramedian and lateral fissures, and posterio-laterally to lateral fissures; central fascia pale brown anteriorly, the posterior end pale sandy brown, centrally black, and splaying out and merging with the mainly black pronotal collar; the black pronotal collar colouration continues around the ventro-lateral pronotal margins with a very narrow pale margin visible; narrow anterior pronotal margin pale brown; lateral angles of pronotal collar ampliate. Mesonotum predominantly black, with submedial sigillae deep brown merging to black medially, lateral sigillae black and merging into deep brown to black mesonotum; only the dark brown along and adjacent to parapsidal suture is more clearly defined; lateral sigillae extend posteriorly to anterior arms of cruciform elevation; area between anterior arms of cruciform elevation black to deep brown; cruciform elevation pale sandy-brown to darker brown, becoming darker towards apices of arms, scutal depressions black; lateral mesonotal margins proximal to, and within wing grooves pale brown; mesonotum with sparse silvery to silvery-yellow pubescence, more pronounced adjacent to wing grooves.

Wings. (Fig. 3B). Fore wings semi-opaque black to brown, relatively darker brown adjacent to all the veins, with conspicuous undulations on the wings between the veins; lengths similar to total body length, with relatively high length/breadth ratios (2.6-3.0); costal vein very gently curved anteriorly towards node; sclerotised zone along anterior costal vein margin similar in width to costal vein width; costal and R+Sc veins fused, but each clearly distinct; nodal line clearly visible in some specimens; CuA vein not intersecting M vein, but directly intersects arculus of basal cell; the three distal vein sections of M that form inner margin of radial cell are generally of unequal length; medial cell larger in size than cubital cell; cubital cell and clavus of similar maximum width; 8 apical cells shorter than adjacent ulnar cells; basal membrane orange and opaque; fore wing venation pale to medium brown; radial cell normally shorter than distance from apex to wing tip (ratios 0.85-1.01). Hind wing predominantly hyaline with variably weak to very weak yellow colouration, always weaker distally; semi-opaque orange plaga covering proximal three-quarters of anal cell 3, the distal margin strongly concavely curved, also covering the proximal third to half of anal cell 2 with obliquely curved or straight margin extending towards vein 2A and further extending adjacent to the vein as narrow colouration to vein termination; the detailed shapes and extents of these areas of orange plaga in anal cells 2 and 3 is variable between individuals; paler orange infuscation variably developed within proximal terminations of cubital cell 1, medial, radial and costal cells, often partially extending weakly adjacent to cubitus, median, subcostal and costal veins; minor weak brown infuscation at distal termination of 2A vein extending very weakly to adjacent margin of anal cell 2; weak but distinct brown infuscation developed along wing margin is commonly present; 6 apical cells; anal cells 1+2+3 much broader than cubital cell 1+2; hind wing venation orange-brown grading to medium-brown apically.

Legs. Fore coxae predominantly black with pale sandy-brown longitudinal fasciae on lateral and posterior faces, and three erect black spines; mid and hind coxae similar but with more extensive pale sandy-brown colouration, especially on posterior faces; fore and mid femora, trochanters, tibiae and tarsi predominantly black, in some specimens dark brown with pale sandy-brown longitudinal fasciae; hind femora dark brown with pale sandy-brown posterior faces; hind trochanters, tibiae and tarsi medium brown with darker brown longitudinal fasciae; claws dark brown, darker apically; three spines on fore femora.

Opercula. (Fig. 3C). Relatively broad, oriented roughly parallel to abdomen, angled inwards towards abdominal midline in disto-medial area; disto-medial operculum margins rounded, the degree of rounding variable between specimens; medial margins reaching margins of tympanal cavity while distal margins and crests not reaching lateral tympanal cavity margins; inner margins of opercula well separated; opercula developed asymmetrically around meracantha; meracantha spikes overlap operculum plate; broad dome developed across distal and basal areas of opercula extending towards crests; dome areas marked by dark brown colouration, remaining colouration pale sandy-brown; opercula may just extend to anterior margin of sternite II in lateral view.

Timbals. (Fig. 4C). Five long ribs, the anterior long rib shortest, commonly not reaching dorsal termination of adjacent anterior short rib, but in some specimens just overlapping the termination; four well developed short ribs; long ribs 1 to 4 fused dorsally to basal spur, but not fused at their ventral terminations; well developed elongated dome on timbal plate with shallow grooves across top of dome.

Abdomen (Fig.1C). Width across auditory capsules greater than head width across compound eyes; in dorsal view, tergites gently tapered posteriorly to tergite 6, more strongly curved and tapered along tergites 7 and especially 8, giving a slightly bulbous shape to abdomen; tergite 2 black dorsally, the black colouration extending submedially along anterior margin and expanding laterally and ventro-laterally on to, and enclosing the auditory capsules, further extending ventrally along the anterior margin of sternite II; submedial area orange to orange-brown; black dorsal pigmentation of tergite 2 extends anteriorly, becoming deep brown, to tergite 1, filling area between timbals; tergites 3 to 7 predominantly bright orange, each with well defined black dorsal areas not extending across intersegmental membranes, and decreasing in size from tergite 3 through to 7; deep brown pigmentation along ventro-lateral margins to at least tergites 3 to 5; the black dorsal area on tergite 8 posteriorly located and extends to pygofer and around whole of posterior margin, with remaining colouration orange. Sternites pale sandy-brown to pale orange-brown, convex but not always fully visible in lateral view; a diffuse

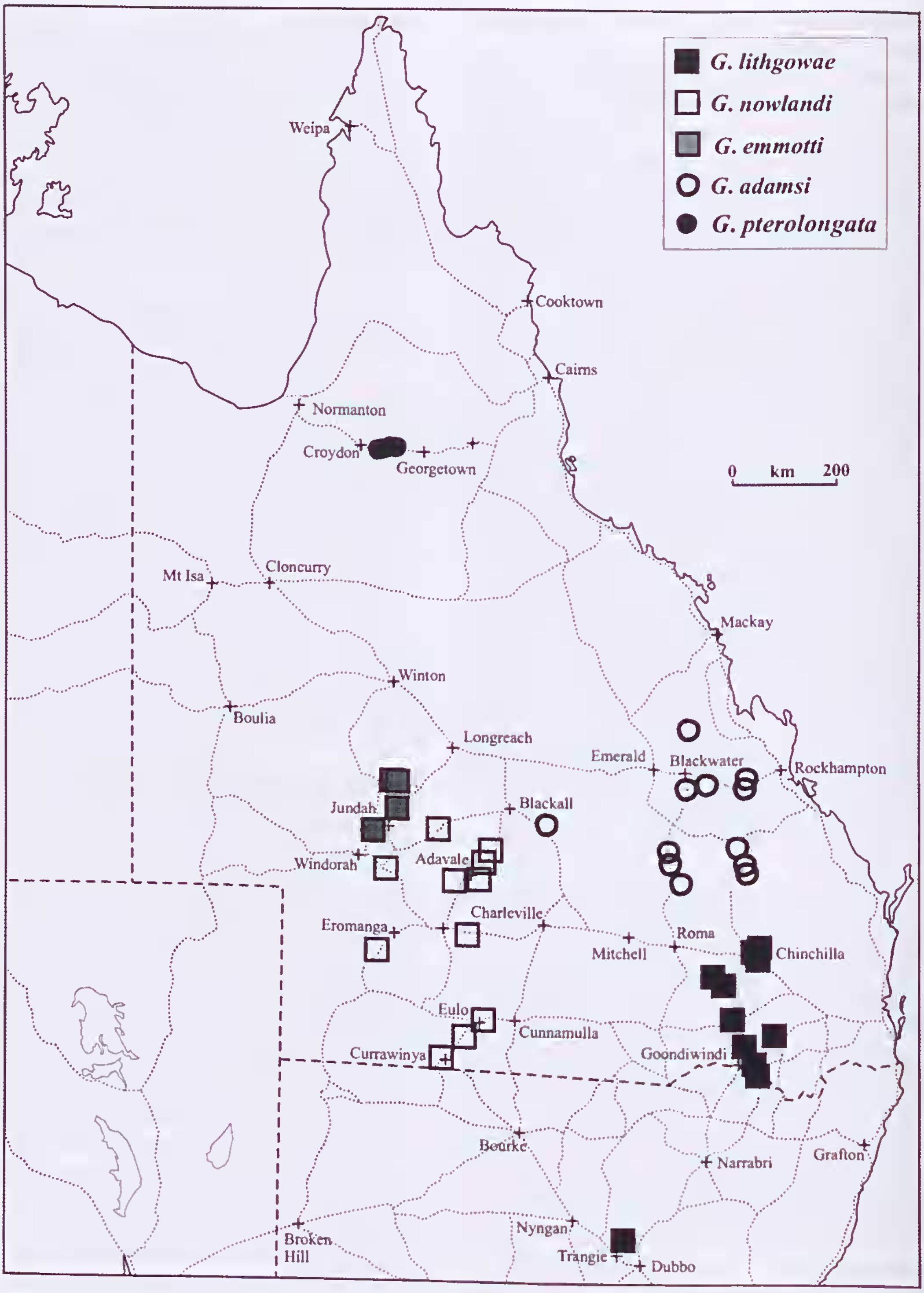


FIG. 7. Distribution records of the five described *Gudanga* species in Queensland and New South Wales based on collected specimens, and aural records and recordings as listed in the text.

and weakly developed brown spot or short fascia on shallow medial depression adjacent to posterior margin of sternite II; diffuse and weakly developed brown abdominal venter on sternites III to V may be present; posterior half of sternite VII black to deep brown, extending to sternite VIII.

Genitalia. (Figs 5C-6C). Pygofer predominantly black to deep brown including dorsal beak; prominent upper lobes extending to anal styles, relatively acutely rounded terminations in lateral view, variable between specimens, which dominate pygofer between basal lobes and dorsal beak; dorsal and especially ventral margins of upper lobe with gentle convex outlines as seen in lateral view; angle between margins of upper lobe and their extension to dorsal beak normally greater than orthogonal (i.e. relatively gently rounded); prominent sharp dorsal beak; well developed basal lobes with rounded apices, visible in lateral view; secondary basal lobes well developed and clearly seen in dorsal and lateral views; robust claspers, sharply pointed, with hooked terminations, tending slightly outwardly pointing; median lobe of uncus conspicuous; aedeagus with tubular theca which in lateral view has a slanting termination, the posterior rim most prominent; a pair of pseudoparameres, slightly curved apically in lateral view, sharply pointed apices, longer than theca, originating closer to theca than its base; theca with short ventral support; aedeagus basal plate undulated in lateral view, Y-shape in dorsal view, and with functional membraneous 'hinge'.

Female (Pl. 3B). Generally similar to male in patterning and colour, with some colour variation between specimens. Head and pronotum very close to male colours and patterning; mesonotum varies from specimens which are similar to male, to those with medium brown colouration of submedial sigillae and enclosing mesonotum area; in such specimens, lateral sigillae dark brown to black, with parapsidal suture visible due to sharply defined paler brown colours. Wings as in male; relatively high length/width ratios (2.8-3.0); radial cells shorter than distance from their apices to wing tip (ratios 0.90-0.96). Legs similar to colour patterning of males, but with reduced areas of black and brown pigmentation and generally paler brown pigmentation replacing the darker male colours. Abdomen: Tergite 1 medium to dark brown; tergite 2 with dorsal dark brown to black patches, not extending submedially in some specimens, grading submedially and laterally to brown or black in other specimens; auditory capsules brown to black; black to brown dorsal patches on tergites 2 to 8 progressively reduce in size posteriorly, variably cross intersegmental membranes, with additional posterior narrowing of individual patches occurring within each tergite; overall appearance of the darker dorsal areas is that of a longitudinal dark fascia, commonly with a conspicuous splaying out anteriorly towards, and within, tergite 2; colour of main areas of tergites 2 to 8 is orange, with narrow brown areas extending along ventro-lateral margins of tergites; tergite 9 pale brown to orange-brown with an ill-defined slightly darker brown broad median fascia not always extending along length of tergite; in addition, a pair of submedial brown diffuse fasciae that extend from anterior tergite margin distally to stigma are present in some but not all specimens; anterior margin of tergite 9 commonly has a zone of brown pigmentation extending and narrowing from submedial to ventro-lateral margins, again not always present; a weak to pronounced brown or black spot occurs posterior-laterally. Sternites uniformly pale sandy-brown to orange-brown, usually with a diffuse and weakly developed brown central fascia, which tends to darken on sternites VII and VIII. Ovipositor sheath extends between 0.6-1 mm beyond apex of tergite 9.

Measurements. N = 27♂, 12♀. Ranges and means (in parentheses): *BL*: ♂ 15.8-20.1 (17.98); ♀ 16.7-20.4 (18.42). *FWL*: ♂ 15.7-18.4 (17.03); ♀ 17.0-18.8 (18.06). *FWW*: ♂ 5.6-6.9 (6.21); ♀ 5.9-6.6 (6.20). *HW*: ♂ 4.5-5.3 (4.94); ♀ 4.8-5.2 (5.06); *PW*: ♂ 4.1-5.0 (4.61); ♀ 4.5-5.0 (4.76). *AW*: ♂ 5.5-6.4 (5.89); ♀ 4.9-5.8 (5.46). *FWL/WR*: ♂ 2.59-2.87 (2.75); ♀ 2.80-3.00 (2.91).

Distribution, Habitat and Behaviour. (Fig. 7) Known only from a restricted region within far south-western Queensland which

TABLE 1. Comparative summary of calling song parameters of the three Queensland *Gudanga* species emitting three echemes per phrase.

Species	Localities	Phrase repetition rates	Intra-phrase repetition rates		Echeme durations (ms)			Inter-echeme intervals (ms)		Macro-syllable durations (ms)	Female response flick intervals (ms)	Extended echeme durations (sec)
			Echemes 1 to 2	Echemes 2 to 3	Echeme 1	Echeme 2	Echeme 3	Echemes 1 to 2	Echemes 2 to 3			
G .emmotti (1) Short echeme 1 lengths (<190 ms)	Bald Hills, Hickleton and Noonbah stations*	Mean = 514±46 ms (1) = 1.95 Hz [298-711] (2) (n=216) (3)	185±22 ms = 5.4 Hz [141-255] (n = 219)	108±13 ms = 9.3 Hz [63-218] (n=217)	108±28 [22-184] (n=230)	33.5±8.4 [22-118] (n=217)	26.9±8.8 [10-107] (n=217)	74.5±12.3 [30-127] (n=217)	75.2±10.6 [27-118] (n=217)	(Coalesced) 4.23±0.38 [3.61-5.00] (n=25)	-	Single 'buzz' only recorded (and heard) = 1.16 sec
(2) Long echeme 1 lengths (<190 ms)	As above	Mean = 633±55 ms = 1.58 Hz [542-772] (n=80)	323±42 ms = 3.1 Hz [261-412] (n= 81)	113±15 = 8.8 Hz [70-205] (n=78)	259±38 [196-349] (n=82)	35.5±14.0 [112-131] (n=78)	28.4±6.4 [10-49] (n=78)	65.4±13.0 [41-88] (n=78)	77.7±13.4 [38-100] (n=78)	(Non-coalesced) 4.92±0.40 [4.02-5.33] (n=48)	-	
G.emmotti (1) Short echeme 1 lengths (<190 ms)	68 km N. Windorah*	Mean = 564±71 ms = 1.77 Hz [446-672] (n=20)	211±34 ms = 4.7 Hz [130-276] (n=22)	113±6 ms = 8.8 Hz [105-124] (n=2)	129±34 [66-180] (n=22)	31.0±3.0 [26-38] (n=22)	24.4±5.5 [14-37] (n=22)	83.3±18.0 [59-115] (n=22)	82.5±6.9 [73-98] (n=22)	Combined with above	46.4 ±3.5 [40-55] (n=21)	None recorded
(2) Long echeme 1 lengths (≥ 190 ms)	As above	Mean = 644±49 ms = 1.69 Hz [591-794] (n=44)	310±37 ms = 3.2 Hz [276-405] (n=45)	114±11 = 8.8 Hz [93-136] (n=45)	243±36 [190-373] (n=45)	27.3±2.7 [18-30] (n=45)	23.7±5.1 [8-31] (n=45)	69.7±9.8 [53-87] (n=45)	87.2±10.8 [74-115] (n=45)	Combined with above		
G. nowlandi	Milroy & Bulls Gully Stations Nr. Adavale; 74 km NNE Adavale (Boss's Gorge)	Mean = 388±37 ms = 2.58 Hz [252-525] (n=59)	126±13 ms = 7.9 Hz [60-153] (n=66)	62±5 = 16.1 Hz [38-76] (n=66)	46.2±10.3 [32-69] (n=66)	28.5±3.1 [21-37] (n=66)	14.2±4.2 [6-21] (n=66)	79.7±11.6 [28-110] (n=66)	34.6±4.4 [26-43] (n=66)	(Coalesced) 4.41±0.52 [3.3-5.3] (n=36)		Mean = 1.25±0.23 sec [0.98-1.40] (n=3)
G. nowlandi	Eulo-Currawinya region	Mean = 411±54 ms(1) = 2.43 Hz [315-643](2) (n=262)(3)	159±27 = 6.29 Hz [120-363] (n=266)	64±8 = 15.6 Hz [56-162] (n=265)	78.8±24.6 [34-300(4)] (n=266)	33.4±4.8 [25-50] (n=266)	22.3±3.5 [12-40] (n=265)	82.3±16.4 [59-146] (n=266)	31.4±5.2 [12-46] (n=265)	Combined with above		Mean = 1.18±0.31 sec [0.43-2.22] (n=142)
G. nowlandi	63 km SW Eromanga*	Mean = 373±20 ms = 2.68 Hz [341-482] (n=110)	126±5 =7.9 Hz [88-146] (n=113)	60±2 =16.7 Hz [55-70] (n=120)	54.0±7.3 [26-79] (n=115)	25.9±3.4 [21-37] (n=121)	18.0±2.9 [13-29] (n=120)	71.9±8.5 [49-108] (n=121)	35.0±3.4 [23-42] (n=120)	Combined with above		Mean = 1.17±0.16 sec [0.90-1.39]

TABLE 1.Continued ...

Species	Localities	Phrase repetition rates	Intra-phrase repetition rates		Echeme durations (ms)			Inter-echeme intervals (ms)		Macro-syllable durations (ms)	Female response flick intervals (ms)	Extended echeme durations (sec)
G. nowlandi	50 km SE Windorah (Jundah-Quilpie Rd Jct)	Mean = 484±33 ms = 2.07 Hz [436-602] (n=155)	154±7 = 6.5 Hz [136-184] (n=165)	97±3 = 10.3 Hz [89-108] (n=165)	77.7±5.1 [64-91] (n=165)	25.7±2.0 [23-36] (n=165)	17.6±1.6 [14-24] (n=165)	76.6±8.8 [62-118] (n=165)	71.9±3.5 [62-82] (n=165)	Combined with above	49.2±3.9 [39-61] (n=33)	None recorded
G. lighgowae	Chinchilla; 20 km E Moonie; 15 km SW Goondiwindi; Southwood N.P. (All data)	Mean = 739±111 ms = 1.35 Hz [531-1143] (n=154)	196±51 = 5.1 Hz [146-412] (n=165)	98±6 =10.2 [80-118] (n=165)	127±52 [76-346] (n=165)	36.5±4.9 [25-58] (n=165)	28.1±3.8 [14-38] (n=165)	69.7±6.6 [51-88] (n=165)	62.0±5.3 [45-77] (n=165)	(Coalesced) 4.04±0.59 [2.4-5.1] (n=38) (lowest values tend to occur at end or start of echemes)	43.9±4.8 [30-54] (n=60)	None recorded
G. lithgowae	As above, with echeme 1 <150 ms only	Mean = 721±89 ms = 1.39 Hz [531-934] (n=138)	181±17 = 5.5 Hz [146-212] (n=148)	97±6 = 10.3 Hz [80-112] (n=148)	112±18 [76-145] (n=148)	36.2±4.3 [25-49] (n=148)	27.8±3.7 [14-38] (n=148)	69.9±6.4 [51-88] (n=148)	61.5±5.2 [45-77 (n=148)	-	-	-

(1) Mean ± 1σ, with equivalent Hz values; (2) Range of values; (3) Number of data (4) Includes atypical longer echemes
* Recordings by D. Marshall; + recordings by D. Marshall, L.W. Popple, A. Ewart.

extends from approximately 68 km north of Windorah (aural records), northward through Stonehenge and further northwest into areas some 15-25 km west of the Lochern National Park, specifically the Noonbah (aural records), Bald Hills and Hickleton Stations. Associated with Mulga (*A. aneura*) and Creekline Mineritchie (*A. cyperophylla*) woodlands. Apparently does not extend west of Windorah into the inter-dune mulga woodlands of the eastern Simpson Desert. A localised species, wary and cryptic. Available records range from January to March. Current distribution records indicate no overlap with *G. nowlandi*.

Etymology. Named after Angus Emmott of Noonbah Station, well known for his extensive and systematic insect collecting through the region, together with his wide natural science contributions to inland Australia.

Similar Species. *G. emmotti* is very similar in morphology and pigmentation to *G. nowlandi*. Subtle differences in their calling songs provided the first indications of complexity and led ultimately to the recognition of their status as sibling species. Both species exhibit variability in their detailed morphology and colouration, enough to preclude most external characters as being uniquely diagnostic.

The most consistent character differences are seen in the respective development of the secondary basal lobes within the pygofer (Figs 5B, C and 6B, C). In *G. emmotti* these are relatively swollen and clearly visible in lateral and dorsal view. In *G. nowlandi*, these are much reduced in size, not markedly swollen and not easily visible. To evaluate these characters require either that the pygofer is very well exposed in preserved specimens, or else requires pygofer dissection.

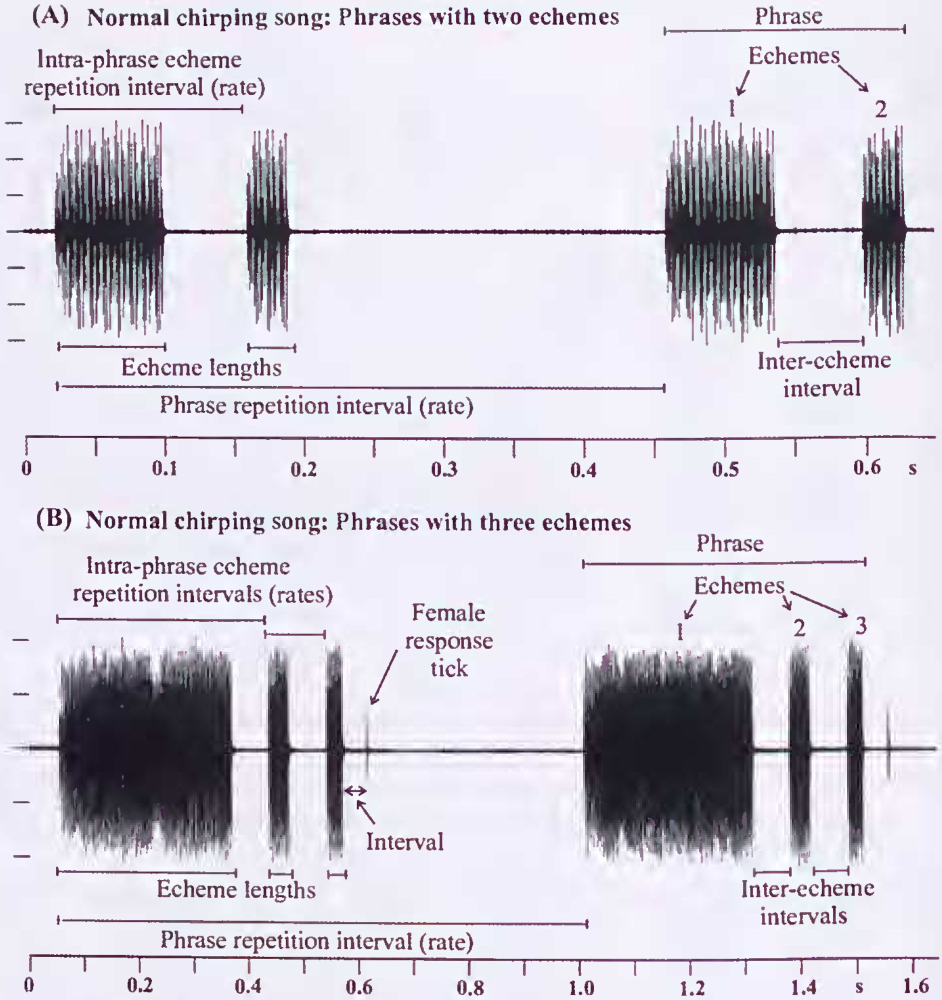


FIG. 8. Waveform plots of the two basic types of normal chirping song of the Queensland *Gudanga* species: (A) Two echemes per phrase (*G. adamsi*), and (B) three echemes per phrase (*G. lithgowae*). The song parameters measured and documented in Tables 1 to 3 are illustrated on the Figure. The vertical scales are linear relative amplitude scales in this and all following waveform plots.

The following, less obviously distinct characters provide useful guides to identification when they are considered in combination and when dissection of the pygofer is not practical:

(i) Upper pygofer lobe shape (as seen in lateral view; Figs 5B, C); G. *emmotti* with relatively more acutely rounded posterior termination, and with gently undulated outlines along dorsal and ventral margins. G. *nowlandi* with more broadly rounded posterior termination, and with slight or even no curvature in outline along dorsal and ventral margins.

(ii) Angle between dorsal margin of upper lobe and its extension towards dorsal beak (as seen in lateral view; Figs 5B, C): For G. *emmotti*, this is broadly rounded and greater than orthogonal; for G. *nowlandi*, it is near orthogonal.

(iii) Opercula shape (Figs 3B, C). For G. *emmotti*, the disto-medial margin tends to be more acutely rounded. For G. *nowlandi*, the disto-medial margin is more broadly rounded and the opercula generally broader in outline.

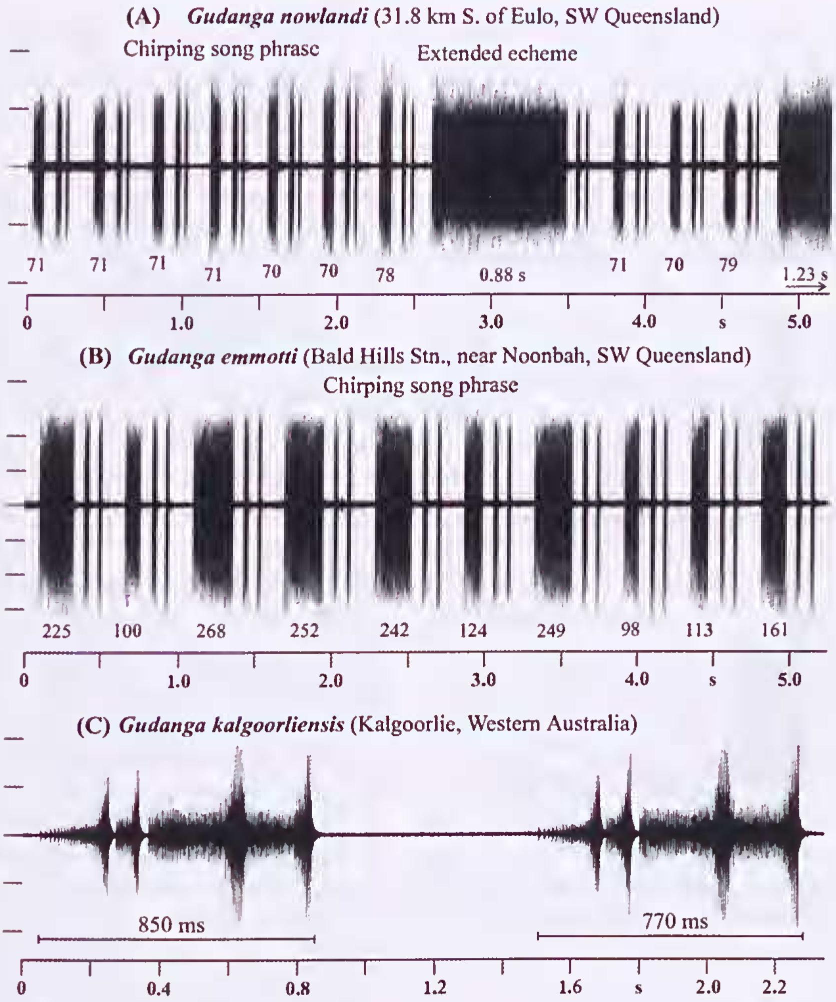


FIG. 9. Waveform plots comparing the similarities and characteristic differences between the calling songs of the three morphologically very similar *Gudanga* species, *G. nowlandi* and *G. emmotti* from south west Queensland and *G. kalgoorliensis* from Western Australia (recording by D. Marshall). The figures beneath the echemes in (A), (B), are the durations (ms), and seconds for the two extended (buzz) echemes in (A).

(iv) Timbal ribs (Figs 4B, C). In *G. emmotti*, the anterior long rib (no. 5) typically does not reach the dorsal termination of the adjacent anterior short rib. In *G. nowlandi*, the anterior long rib more commonly extends to, and overlaps with, the adjacent anterior short rib.

Song differences are detailed below.

SONGS OF THE QUEENSLAND *GUDANGA* SPECIES (FIGS 8-17).

General Characteristics. The calling songs of each of the five species are predominantly complex chirping songs, with an additional interspersed extended 'buzz' echeme commonly emitted within the calling songs of *G. pterolongata* and *G. nowlandi*, most conspicuously during the warmer parts of the day (later morning through to later afternoon), and when the cicada populations

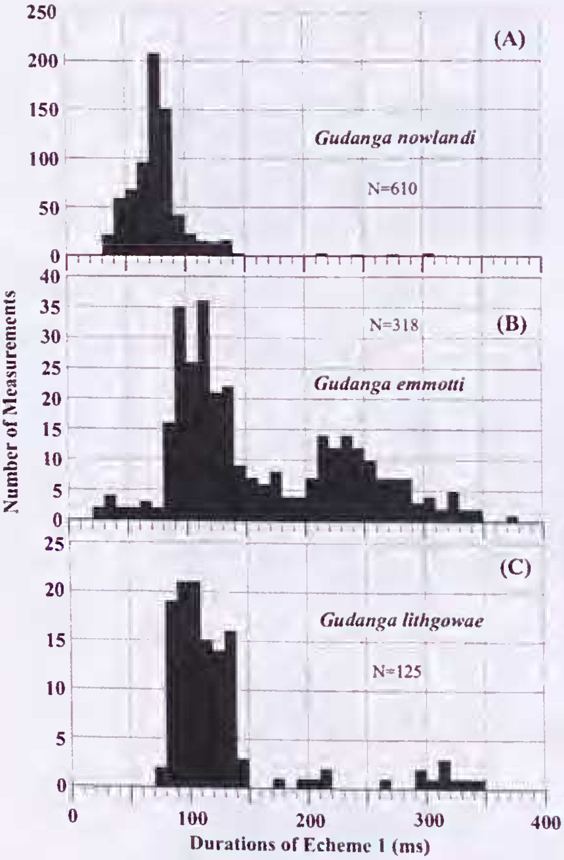


FIG. 10. Histograms comparing the distributions of the echeme 1 durations in the three-echeme chirping song types emitted by *G. lithgowae, G. nowlandi and G. emmotti.*

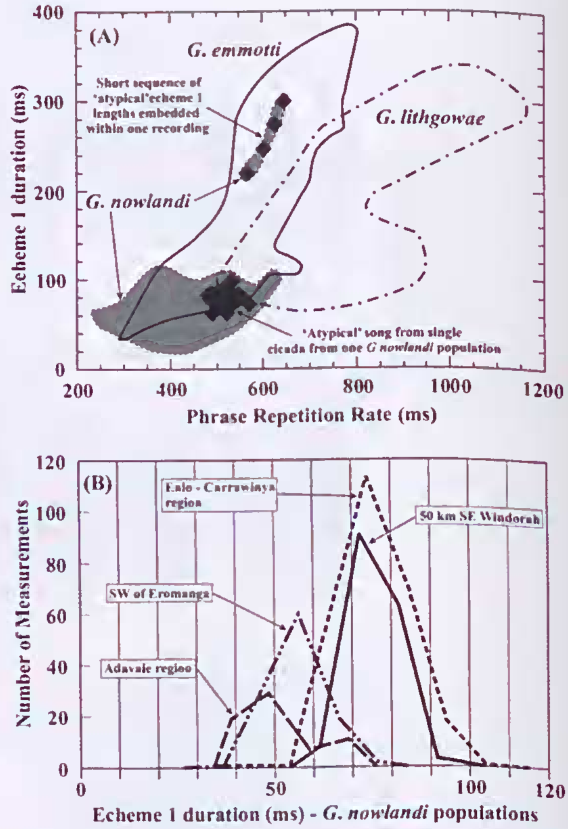


FIG. 11. (A), echeme 1 duration versus phrase repetition rate within the three species emitting the 'three-echeme' chirping song types. Also shown are two sets of 'atypical' song data recognised by statistical analyses within the *G. nowlandi* songs. (B), distribution of echeme 1 durations within four major population groupings of *G. nowlandi*, illustrating subtle inter-population shifts.

are relatively high. The chirping song consists of repeated chirp phrases, each phrase comprising either two or three echemes depending on species. These song differences provide a clear division between the five *Gudanga* species occurring in Queensland; the three-echeme song types include *G. lithgowae*, *G. nowlandi* and *G. emmotti*, while the two-echeme song types include *G. adamsi* and *G. pterolongata*. Fig. 8 illustrates the detailed nomenclature and the specific temporal parameters used to describe the songs in this paper.

The Three-Echeme Song Types

The echemes are simply labelled 1, 2 and 3. The initial echeme (echeme 1) is the longest, echeme 3 is normally the shortest, and echeme 2 intermediate in duration (Table 1). Differences in the durations of the echemes, the phrase repetition rates, the inter-echeme intervals and the intra-echeme repetition rates (Fig. 8) between the species, shown below, are assumed to be sufficient to allow female cicadas to recognise conspecifics. They also facilitate taxonomic identification.

As indicated by the morphological descriptions given above, *G. nowlandi* and *G. emmotti* are sibling species, not easily distinguished by colour or morphology. Figs 9A, B, illustrate the gross temporal structures of their calling songs. The chirping song phases of these two species are characterised by differences in the durations of echeme 1. Additionally, *G. nowlandi* commonly emits extended buzz echemes, between 0.43-2.25 seconds in length, which are very rare in the *G. emmotti* songs. It is noted that the longest measured echeme 1 (0.38 second) in a *G. emmotti* song is shorter than the shortest measured buzz echeme in *G. nowlandi*. A third morphologically very similar species is described from Western Australia, *G. kalgoorliensis* Moulds, whose calling song is shown for comparison in Fig. 9C. Not only is this song very different from the two Queensland sibling species, but it exhibits quite different temporal phrase structures from all of the known Queensland *Gudanga* species.

The complexities of the *G. emmotti* song are illustrated in Figs 10B, 11A and 14 (see Table 1). The variability of echeme 1 durations is noted above, the distribution of the durations being broadly bimodal, with the critical dividing duration lying at approximately 190 ms. These echeme 1 durations range between the extremes of 22 to 373 ms. There is a tendency, observed qualitatively in the field, for a larger proportion of longer examples of echemes 1 to be emitted on hotter days. In any given recording, however, the shorter and longer versions of echeme 1 may roughly alternate (e.g. Fig. 14A), or occur in groups of longer or shorter echeme lengths. There is no clear correlation between the lengths of echeme 1 and the lengths of the associated second and third echemes within each phrase.

For *G. nowlandi*, echeme 1 durations are more closely constrained (Fig. 10A) and typically even shorter than the short examples of echeme 1 produced by *G. emmotti*. Nevertheless, in a single recording from the Eulo-Currawinya area, a small number of unusually extended versions of echemes 1 are found, as discussed below (apparently a rare case of song variation for this species). The echeme 1 durations do, however, show small differences between the main *G. nowlandi* populations for which data are available (Fig. 11B; Table 1). In addition to echeme 1 durations, four other temporal song parameters vary between these two sibling species, namely phrase repetition rates, echeme 1 to 2 repetition rates (noting that the definition of these two parameters partially correlate them with echeme 1 length; Figs. 8B, 9A), echeme 2 to 3 repetition rates and to a less extent, inter-echeme 2 to 3 intervals. The other very important characteristic difference is the presence of extended 'buzz' echemes that are present in most, but not all, *G. nowlandi* song sequences (Figs 12B-C, 13A). These, however, are emitted most strongly and frequently in hot weather and where high population densities of this cicada occur. At lower population densities, even in hot weather, the 'buzz' phrases are typically absent. The points of insertion of the extended 'buzz' echemes into the normal chirping song are generally consistent. When emitted, they occur between echemes 1 and 2 (Figs 12C, 13A), with echeme 1 typically clearly defined and produced just prior to the 'buzz', and with echemes 2 and 3 following thereafter. In some records, echeme 1 is partially or fully coalesced into the following 'buzz' echeme (Fig. 12B). As also seen in Figs 12B and C, echeme 1 durations that immediately precede the extended 'buzz' phrases are usually of slightly longer duration than those emitted elsewhere in the chirping songs. As noted, the emission of extended 'buzz' echemes by *G. emmotti* is very rare, with only one recorded (Table 1).

The song of *G. lithgowae* shares broad characteristics with that of both *G. nowlandi* and *G. emmotti*, but is statistically distinct (see below). Echeme 1 durations are longer on average than in *G. nowlandi*, with some sporadically produced longer echemes being more closely similar to *G. emmotti* (Figs 10C, 15A, B). Further differences within the *G. lithgowae* song, compared to *G. nowlandi* and *G. emmotti*, include phrase repetition rates (Fig. 11A), intra-echeme repetition rates, and slightly longer echeme 2 and 3 durations (Table 1).

Finer Scale Macrosyllable Structures. The chirp and extended 'buzz' echemes comprise sequences of partially to completely coalesced macrosyllables in the songs of each species. Figs 14B-D illustrate a rare example, occurring at the initiation of a chirping song sequence of

TABLE 2. Comparative summary of calling song parameters of the two Queensland *Gudanga* species emitting two echemes per phrase

Species	Localities	Phrase repetition rates	Intra-phrase echeme repetition rates	Echeme durations (ms)		Inter-echeme intervals (ms)	Macrosyllable durations (ms)	Extended echeme durations (sec)
			Echemes 1 to 2	Echeme 1	Echeme 2	Echemes 1 to 2		
G. adamsi	35 km S. Blackwater, (Central Queensland)+	Mean= 457±33 ms = 2.19 Hz [357-601 ms] (n=142)	119±7 ms = 8.38 Hz [103-176 ms] (n=32)	43.7±6.2* [31-58] (n=145)	17.8±4.8 [7-40] (n=147)	75.0±6.7 [14-87] (n=147)	4.47±0.67 [3.95-5.89] (n=42) (1.72-3.97 at echeme ends)	No aural record
G. adamsi	Blackdown, Wyseby+ Tambo+, Isla N.P., (Central Queensland)	Mean= 496±36 ms = 2.02 Hz [426-612 ms] (n=114)	142 ±7 ms = 7.04 Hz [125-154 ms] (n=122)	65.8±9.0 [45-83] (n=122)	25.1±4.1 [16-33] (n=122)	76.9±7.9 [56-89] (n=122)	Combined with above	No aural record
G. pterolongata	41 and 60 km E. Croydon, (Northern Queensland)	Mean= 457±32 ms = 2.19 Hz [394-553 ms] (n=181)	121±10 ms = 8.26 Hz [99-138] (n=119)	55.1±5.4 [40-77] (n=119)	38.6±6.5 [31-61] (n=119)	66.9±8.4 [46-83] (n=119)	'Double' Macrosyllables: 10.06±0.80 (n=72) [9.11-12.7] (3.8-7.7 at echeme ends): Single macrosyllables 5.36±0.85 (n=49) [3.8-7.2]	2.55±1.61 [0.65-5.16] N=36

Figures in square brackets are minimum and maximum measured values.

* Excludes two high values of 112 and 127 ms.

+ Recordings by D. Marshall

TABLE 3. Comparison of calling song parameters between the 'anomalous' song of a single recording and the normal songs of *G. nowlandi*, all from the Eulo-Currawinya area (see text for explanation)

Species	Phrase repetition rates (ms)	Intra-phrase echeme repetition rates (ms)		Echeme lengths (ms)			Inter-echeme intervals (ms)	
		Echemes 1 to 2	Echemes 2 to 3	Echeme 1	Echeme 2	Echeme 3	Echemes 1 to 2	Echemes 2 to 3
Normal song type (excluding two sets of anomalous songs)	397±35(1) [315-622](2) n= 233(3)	153±11 [120-205] n=235	63±7 [56-162] n=235	76±9 [34±103] n=235	33±5 [25-50] n=235	22±3 [15-40] n=235	78±9 [59-146] n=235	30±5 [12-46] n=235
Anomalous song type comprising whole of recording (representative subset)	518±21 [479-568] n=26	199±7 [178-210] n=27	77±2 [73-82] n=27	79±8 [64-99] n=27	38±2 [34-42] n=27	23±5 [12-29] n=27	122±9 [103-138] n=27	40±3 [35-45] n=27

(1) Mean ±1σ (2) Range of values (3) Number of data

G. emmotti, in which the macrosyllables comprising each echeme are not coalesced, being clearly separate, thereby showing details of their structures, each macrosyllable comprising four discrete syllables. The frequency structures within the macrosyllables and syllables shown in Fig. 13B-C (*G. nowlandi*), and 14D (*G. emmotti*) are not, however, constant. In the case of *G. emmotti*, the frequencies of the first three syllables lie between *ca.* 8245-9910 Hz, the final syllables >10,600 Hz. This frequency structure is consistent within all macrosyllables examined and facilitates the recognition of macrosyllables structures when strongly coalesced. Figs 14E, F illustrate the progressive processes of syllable and macrosyllable coalescence in the *G. emmotti* songs, in which the syllables are initially still clearly defined (Fig. 14C, E), becoming more compacted as coalescence increases. At a more advanced stage, the microsyllables become segregated into pairs (Fig. 14F), with consequent decease in the macrosyllable lengths (relative to uncoalesced macrosyllables). When examined in time expanded detail, each coalesced macrosyllable is still seen to terminate with a syllable of higher frequency.

Very similar macrosyllable and syllable structures and their frequency variations are observed in the time expanded echeme structures within the songs of *G. nowlandi* (Figs 13B, C) and *G. lithgowae* (Figs 15C). The songs of the latter species appear to be more variable, with syllable structures often less easily resolved, syllables apparently varying between three to five per macrosyllable. Nevertheless, as in the previous songs, rapid frequency modulations are apparent at time expanded detail with an increase in frequency occurring at the termination of each macrosyllable. In the specific example illustrated (Fig. 15C) of an echeme 3 structure, the measured waveform frequencies range between 5.2-9.4 kHz (in fact, even wider, due to greater pulse frequency variability that occurs within the time scales even finer than the time divisions shown). The measured frequency range is consistent with that of the accompanying amplitude spectrum for this same echeme 3 (Fig. 15D). Corresponding macrosyllable durations (and ranges) are similar for the each of the three described species (Table 1), mean values being 4.0, 4.4 and 4.2 ms, respectively, in the *G. lithgowae, G. nowlandi, and G. emmotti songs.*

TABLE. 4. Results of statistical analyses of non-parametric song parameters, calculated according to Chi-Square Kruskal-Wallis procedure

	Phrase Repetition Rates	Intra-phrase echeme repetition rates			Echeme durations (ms)			Inter-echeme intervals (ms)		
		Echemes 1 to 2	Echemes 2 to 3	Echeme 3 to end of phrase	Echeme 1	Echeme 2	Echeme 3	Echemes 1 to 2	Echemes 2 to 3	Echeme 3 to end of phrase
Raw song parameter comparisons										
G. emmotti vs *G. nowlandi*										
Chi-Square	465.8	495.6	570.3	81.6	509.3	72.9	326.4	35.1	475.7	30.7
Asymp. Sig.	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G.emmotti vs. *G. lithgowae*										
Chi-Square	179.848	51.1	187.2	246.0	25.6	36.1	8.25	3.69	220.9	246.0
Asymp. Sig.	.000	.000	.000	.000	.000	.000	.004	.055	.000	.000
G. nowlandi vs *G. lithgowae*										
Chi-Square	287.0	192.3	165.4	287.1	278.3	138.6	230.1	65.9	73.4	286.6
Asymp. Sig	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
Comparisons between recordings with female wing-flick responses following each phrase										
G. emmotti vs. *G. nowlandi*										
Chi-Square	33.7	34.7	38.3	0.59	34.3	22.3	28.8	9.39	36.9	1.69
Asymp. Sig.	.000	.000	.000	.445	.000	.000	.000	.002	.000	.194
G. emmotti vs. *G. lithgowae*										
Chi-Square	39.25	10.9	18.6	43.5	12.1	37.5	9.23	7.03	43.5	43.5
Asymp. Sig.	.000	.001	.000	.000	.001	.000	.002	.008	.000	.000
G. nowlandi vs *G. lithgowae*										
Chi. Square	47.1	48.0	29.4	47.1	48.0	48.4	48.3	1.20	21.1	47.1
Asymp. Sig.	.000	.000	.000	.000	.000	.000	.000	.274	.000	.000

All data shown with 1 degree of freedom. Grouping variable: (Category). Asymp. Sig., asymptotic significance, represents critical ($p(0.5)$) for these statistics.

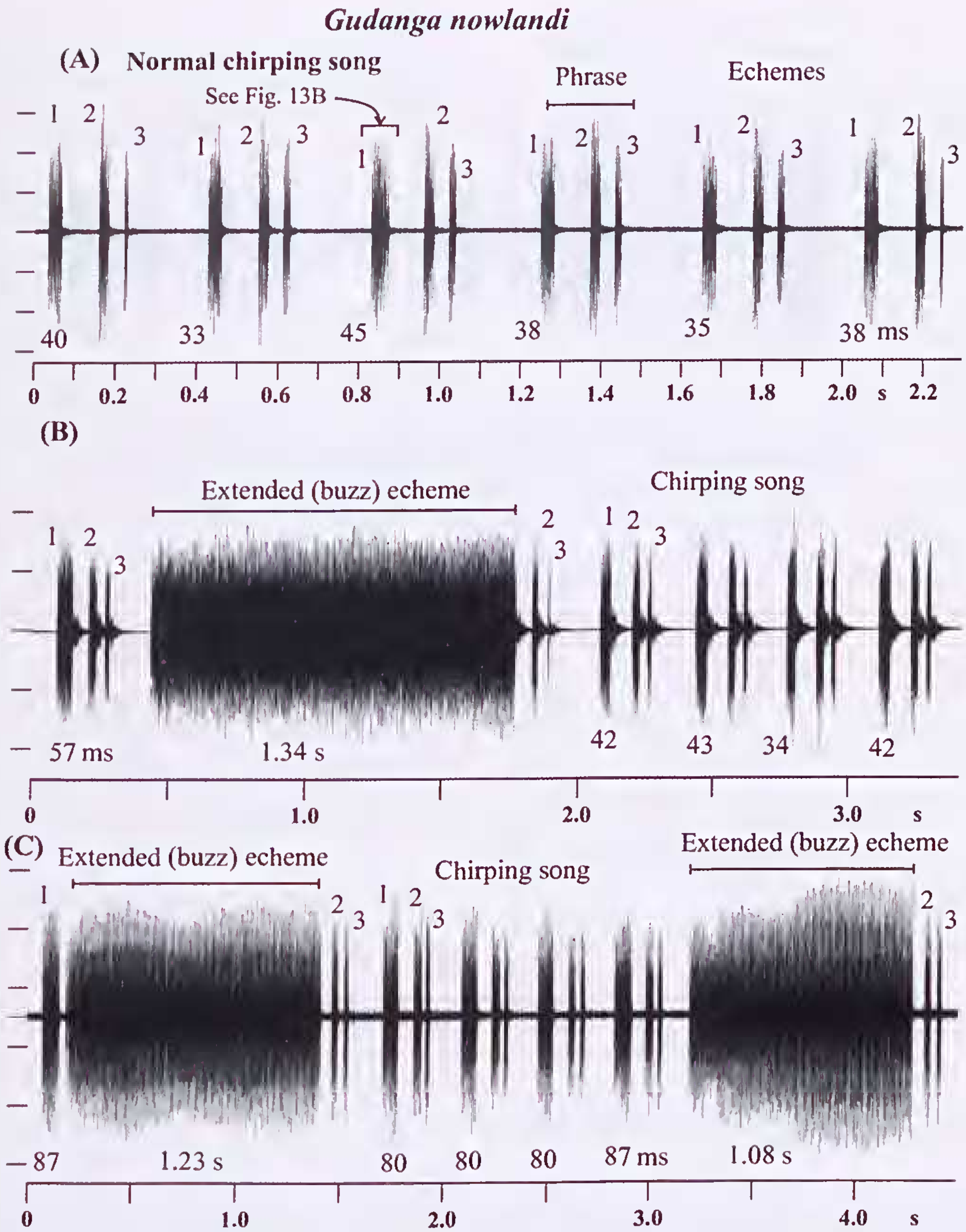


FIG. 12. *Gudanga nowlandi*. Waveform plots showing; (A) the chirping song phase, each phrase consisting of 3 echemes of variable but generally short durations. (B) Chirp phrases with an interspersed extended ('buzz') echeme, and (C) chirp phrases with two interspersed extended echemes. The numbers 1, 2, and 3 indicate the echeme number; numbers beneath the echeme 1's are durations in ms, those beneath the extended echemes are in seconds; A, field recording from Boss's Gorge, 1.xii.1995, ~75 km N. Adavale, south west Queensland. B, container recording at Milroy H.S., near Adavale, 9.i.2000. C, field recording, 31.8 km south of Eulo (Hungerford Road), 18.i.2010, south west Queensland. These were filtered to 1 kHz to improve visualisation.

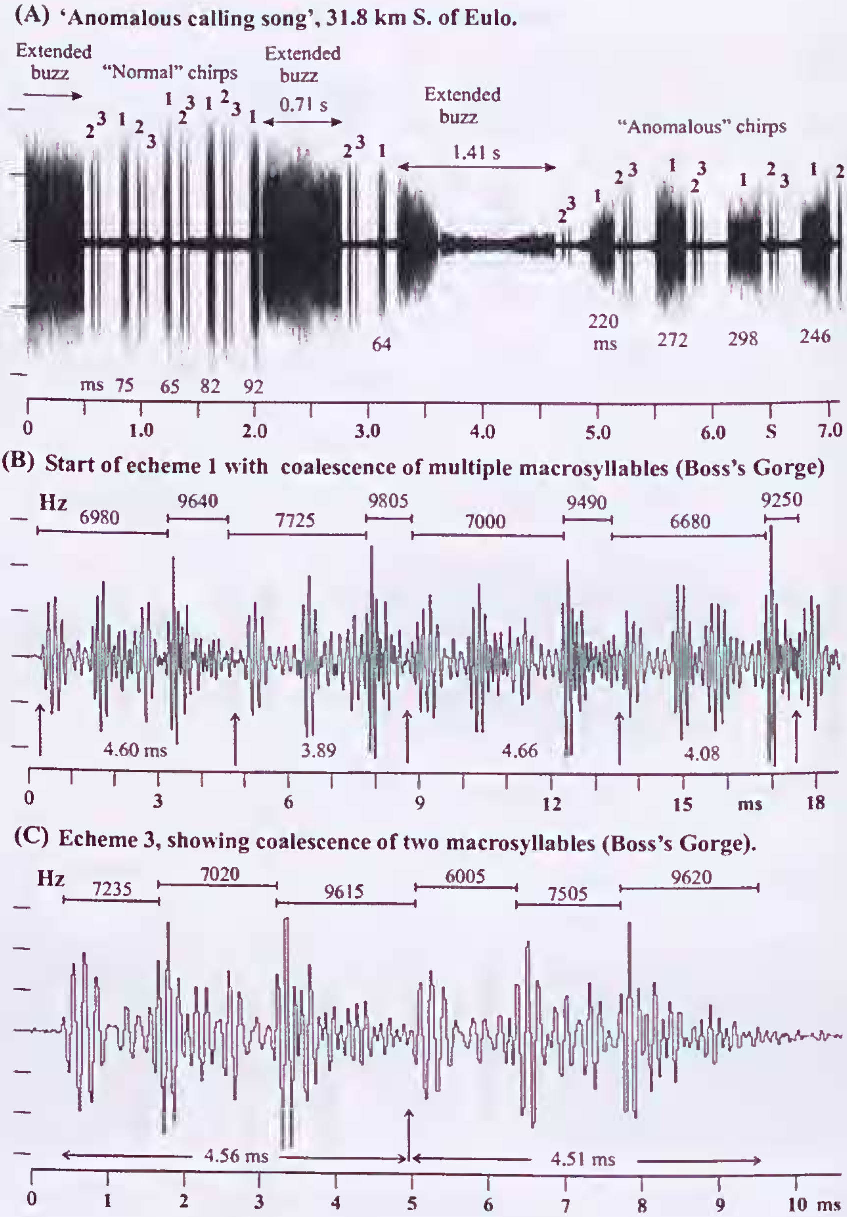


FIG. 13. *Gudanga nowlandi*. Waveform plots showing; (A), complete recording showing a transition from an initial typical chirping song with extended 'buzz' echemes, to an 'atypical' chirping song in which, following the third extended echeme, the first echemes are of longer than normal duration. Numbers above echemes are the echeme numbers, those beneath the echeme 1's are durations (ms). Between 3.5 to 5.0 seconds, the recorded cicada moved its singing position, resulting in the temporary amplitude drop. (B), (C), time expanded plots of detailed syllable-macrosyllable structures within the initial segment of an echeme 1, and a complete echeme 3, respectively. Frequencies measured on these plots from within the syllable segments are shown above the waveforms. Vertical arrows mark the inferred limits of each macrosyllable, with durations in ms. Field recordings from south west Queensland, (A), 31.8 km south of Eulo, 18.i.2010; (B), (C), Boss's Gorge, ~75 km north of Adavale, 1.xii.1998. These were filtered to 2 kHz to improve visualisation.

It is noted, however, that in the *G. lithgowae* songs, slightly shorter than normal syllables commonly mark the beginning and end of each macrosyllable, a distinction from the songs of the other two species.

Amplitude Spectra (Figs 16, 17). The linear frequency spectra of all three species are broadband, with multiple maxima, exhibiting a crude periodicity in some of the *G. nowlandi* and *G. emmotti* spectra. The dominant frequency ranges and means shown by these spectra for each of the three species are very close, lying between approximately 5.4-11 kHz, also representing various localities for *G. nowlandi* and *G. emmotti*. The wide frequency range of the songs is suggested to be an adaptation to their mobile and fast moving behaviour, and the relatively dense acacia woodland in which they occur, thereby facilitating more effective transmission of at least part of the emitted signals. The apparent sidebands, based on detailed measurements of the spectra, reveal a series of low frequency sidebands most likely correlated with repetition rates of the phrases, while the higher frequency sidebands (>200 Hz) possibly reflect the macrosyllable and syllable structures. The inter- and intra-phrase echeme repetition rates broadly correlate with the sidebands in the 6-18 Hz range.

Female Response Clicks. Figs 8B, 15A show an example of female response wing-flicks to the male chirping song of *G. lithgowae*. The response flicks occur 30-54 ms (mean 44 ms) following the emission of the final (third) echeme of each phrase. This behaviour comprises an acoustic duet, the female responding to the structured phrases with wing-flick signals emitted at specific points during the end of each phrase (Sueur & Aubin 2004). It has been described as the 'cueing' (Cooley & Marshall 2001) or 'lilting' (Popple *et al*. 2008) song components. They are believed to facilitate the localisation of the females by the males. Comparable response flicks have been recorded in *G. emmotti* songs from 68 km north of Windorah, and in *G. nowlandi* songs from 43 km southeast of Windorah. The mean response intervals measured are 46 and 50 ms respectively (Table 1), each wing flick following the termination of echeme 3 as in *G. lithgowae*.

Statistical Analyses of Song Specificity within the Three Echeme Song Types.

Methodology. The statistics were based on the measurements of eight song parameters (see Table 4; Fig. 8): echeme 1, 2 and 3 durations, inter-echeme gap 1 duration, inter-echeme gap 2 duration, phrase repetition rate, intra-phrase gap 1 repetition rate, and intra-phrase gap 2 repetition rate.

Some of these parameters are not, however, entirely independent; specifically the repetition rate parameters are dependent on echeme and gap durations (Fig. 8). The data have therefore been subdivided into two subsets, one based on rates and the other based on durations of all echemes and gaps. There were six parameters in the durations analyses (comprising the three echemes and each of the gaps between them; Fig. 8) and three in the rates analyses (each of the three echemes in combination with their subsequent gap). The duration of the silence at the end of each phrase was obtained by summing the durations of the echemes and gaps and then subtracting these from phrase repetition rates (i.e. total phrase lengths).

These measurements were taken from all available replicates (n=2-63) in each recording, across 54 separate recording instances (n=7 for *G. emmotti*, n=33 for *G. nowlandi*, and n=14 for *G. lithgowae*). The recording instances were sourced from several sites across the geographical distributions of these three closely related *Gudanga* species (Fig. 7). For each recording instance, the measurements of each song parameter were averaged and the data were formatted into a song parameters matrix. Within this matrix, song instances were treated as objects and the nine sets of measurements were the attributes.

Data were analysed using PC-Ord software (McCune and Mefford 2006). The outlier analysis, as well as the object and attribute summaries, did not reveal any outliers in the data matrix, which indicated that data exclusion and/or transformation were not required. The Sørensen (Bray Curtis) distance measure was used to generate the distance matrix, as it emphasises absolute differences between individual instances across each of the measures and is

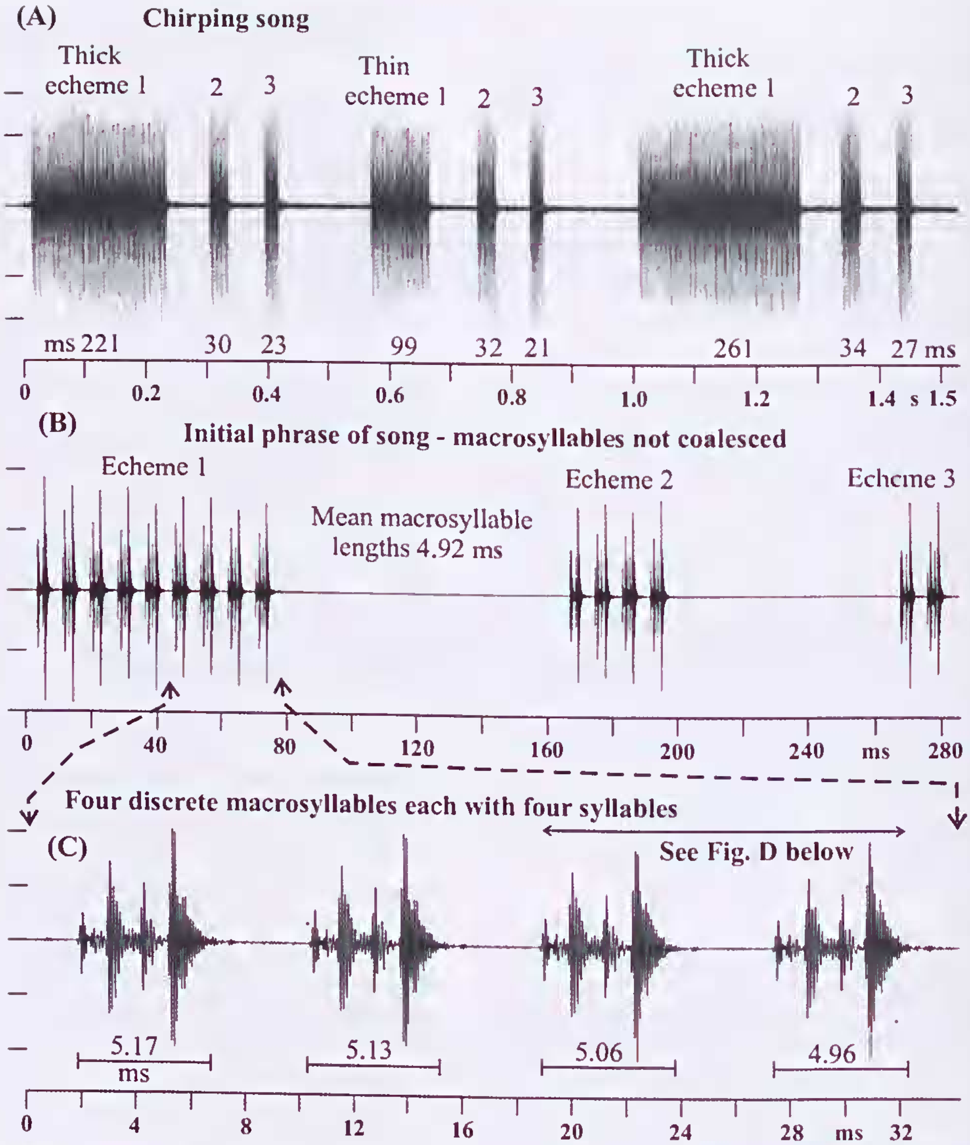
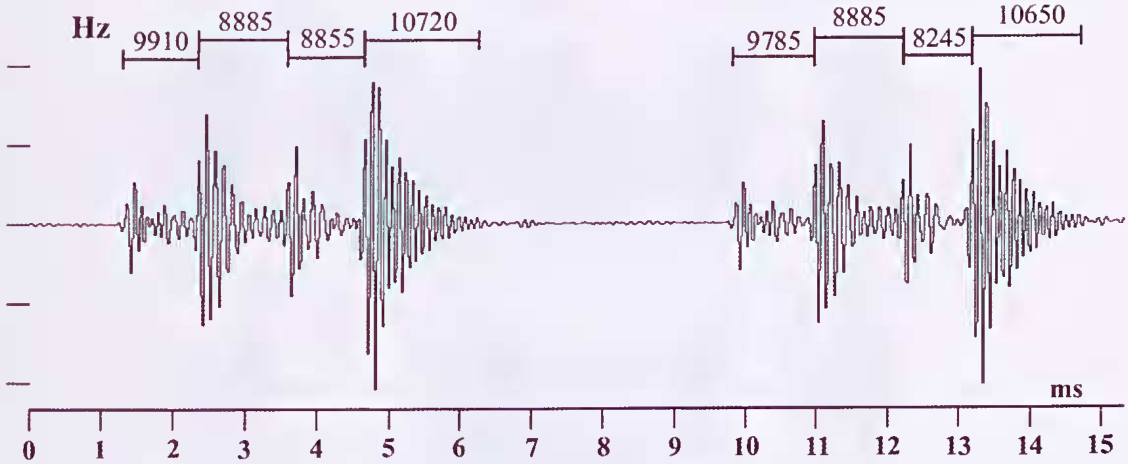
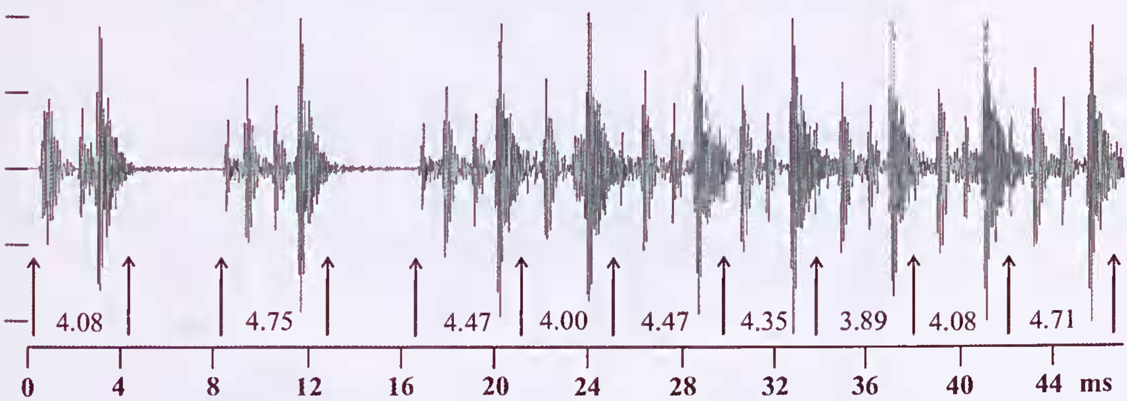


FIG. 14. (Above & opposite) *Gudanga emmotti*. Waveform plots showing, (A) short segment of chirping song illustrating the variable echeme 1 durations. Numbers above echeme are the echeme number, the numbers below the echemes are durations (ms). (B), (C), (D) are time expanded waveform plots of an echeme 1 from the opening phrase segment showing a set of three completely uncoalesced echemes, not commonly seen, illustrating their detailed macrosyllable and syllable structures. (C), (D) show more detailed time expansion revealing the syllable structures and frequencies measured within the pulses of the final two echeme 1 macrosyllables (D). (E), initiation of another echeme 1 from within the same set of recordings showing the progressive process of macrosyllable coalescence, the initial two macrosyllables still separated, the following macrosyllables coalesced into a continuous echeme sequence. (F), final echeme 1 segment, from same song sequence, showing a more advanced stage of macrosyllable coalescence, in which macrosyllables themselves merge into doublets, forming distinctive sets of double macrosyllables. Recordings taken from cicada placed in an open net, in the field, Bald Hills Station, 200 m west of Green Creek, 30.i.2009, south west Queensland. Recording filtered to 2 kHz to improve visualisation.

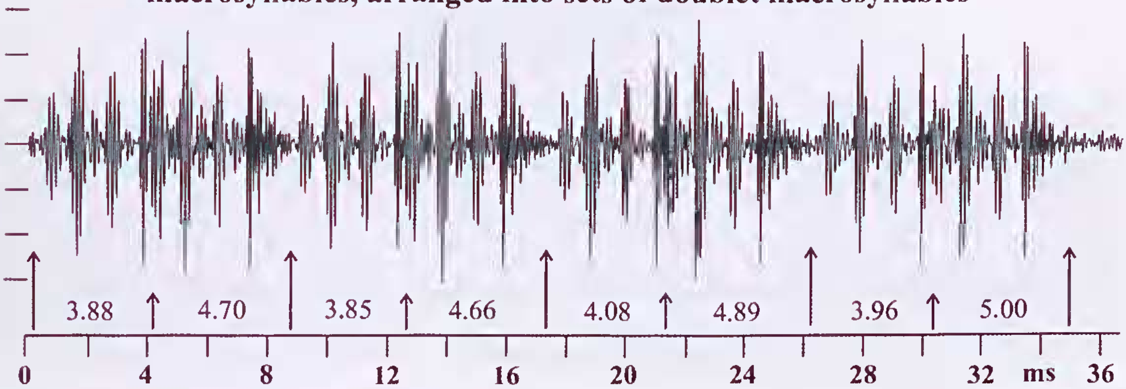
(D) Final two discrete macrosyllables of echeme 1 (see Fig. C).



(E) Start of an echeme 1 showing the initiation of the coalescence of the macrosyllables



(F) End segment of an echeme 1 with partially coalesced macrosyllables, arranged into sets of doublet macrosyllables



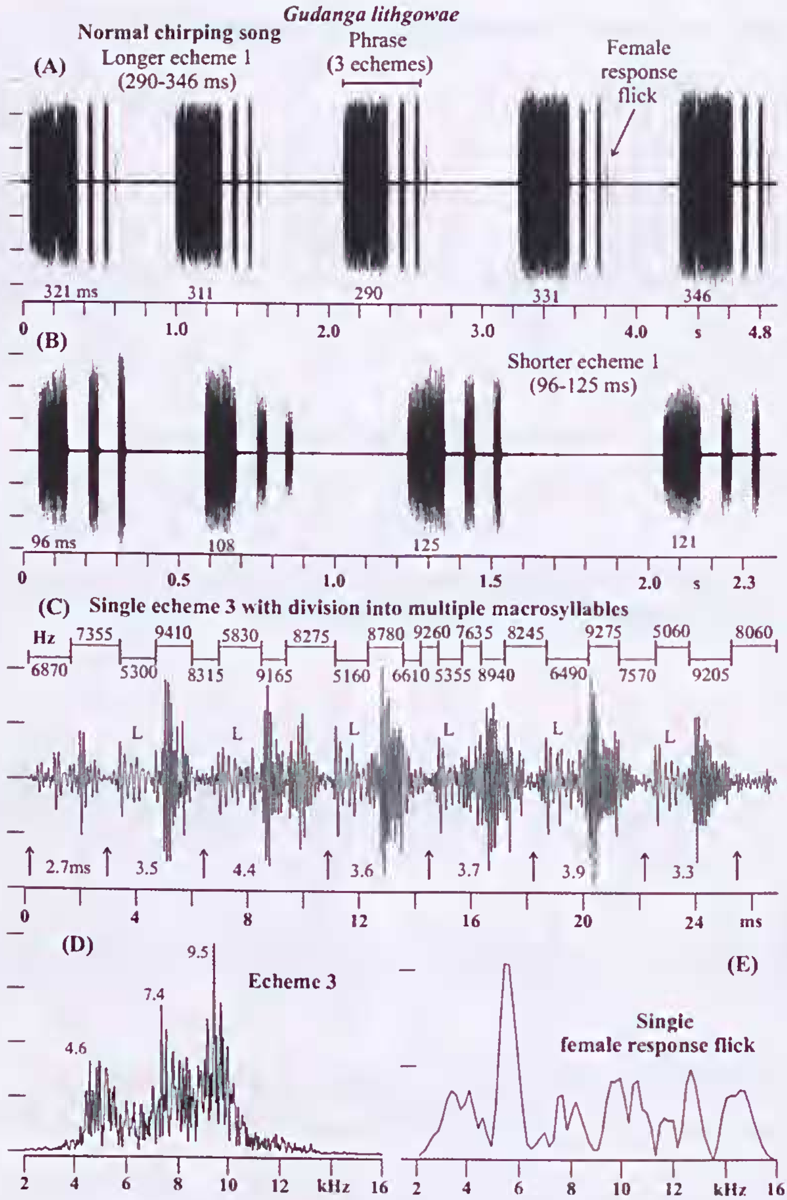


FIG.15. *Gudanga lithgowae*. Waveform plots of (A, B) the gross chirp song structures, each phrase consisting of 3 echemes (1, 2, and 3 in order of emission), with female "wing-flick" responses punctuating the silent intervals following echeme 3 (A only); numbers beneath each echeme 1 are durations in ms. (C) Time expanded detail of a selected complete echeme 3 showing the macrosyllable and syllable structures, and the frequencies measured within the constituent syllables; the upward pointing arrows define the inferred individual macrosyllable limits, with their durations in ms; the symbols 'L' indicate segments of lower frequency. Each macrosyllable is interpreted to consist of three syllables, in some macrosyllables exhibiting variable degrees of syllable coalescence. (D) Amplitude spectrum of the echeme 3 shown in (C). (E) Amplitude spectrum of a single female response flick. Field recordings, filtered to 1 kHz, taken (A, B, E) at the 'Allinga' Property, Chinchilla, south east Queensland, 9.i.1994; (C, D) taken at Southwood National Park, southern Queensland, by D. Marshall, 31.xii.2008.

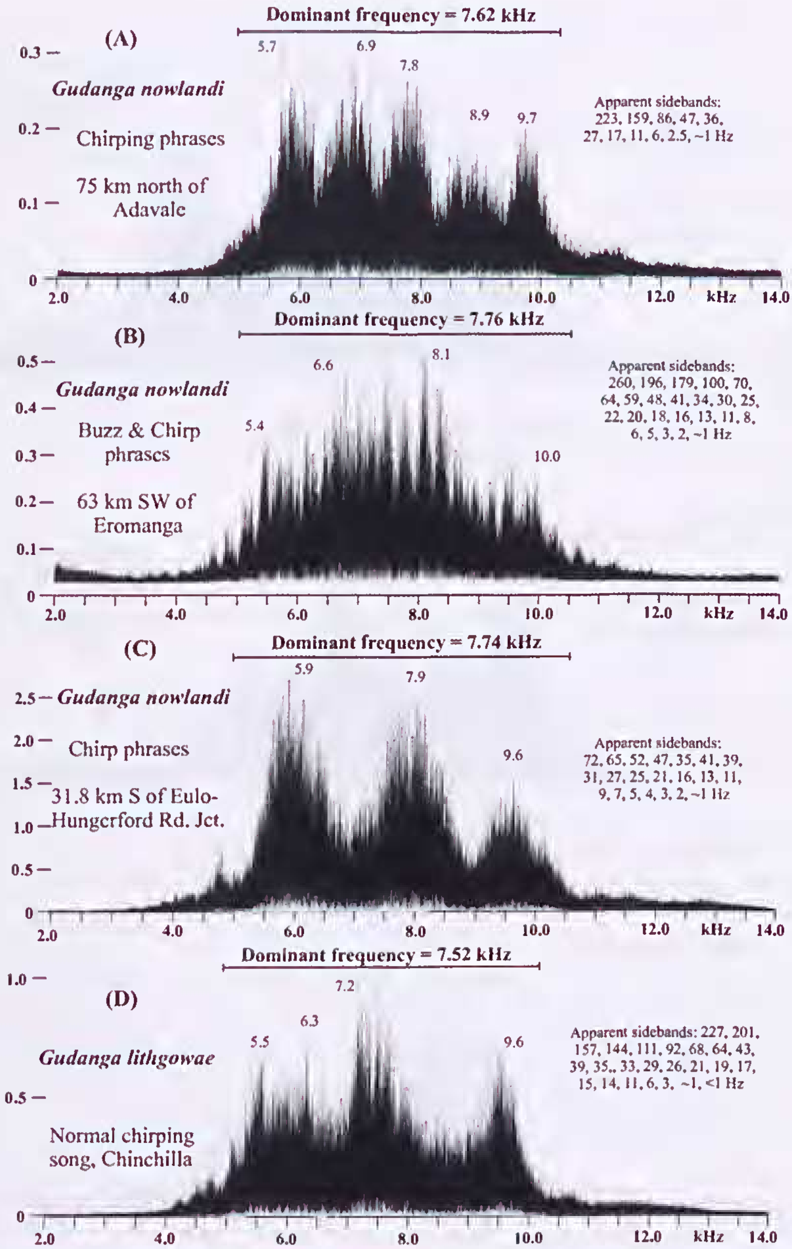


FIG. 16. Amplitude spectra showing, (A) to (C) the frequency distributions within the calling songs of *G. nowlandi* from three widely separated locations within south west Queensland; and (D), *G. lithgowae* from Chinchilla, south east Queensland. The dominant frequency is defined by the mean frequency of the main frequency envelope in each plot, shown by the horizontal lines. The numbers against the various peak concentrations are the maximum frequency (kHz) shown by each main peak. Also listed are the apparent sidebands as measured within each spectrum. Each spectrum is based on field recordings; (A), Boss's Gorge, ~75 km north of Adavale, 1.xii.1998; (B), 63 km south west of Eromanga, 3.ii.2009, D. Marshall; (C), 31.8 km south of Eulo, 18.1.2010; (D), 'Allinga' Property, Chinchilla, 9.1.1994. The vertical scales are linear relative amplitude scales.

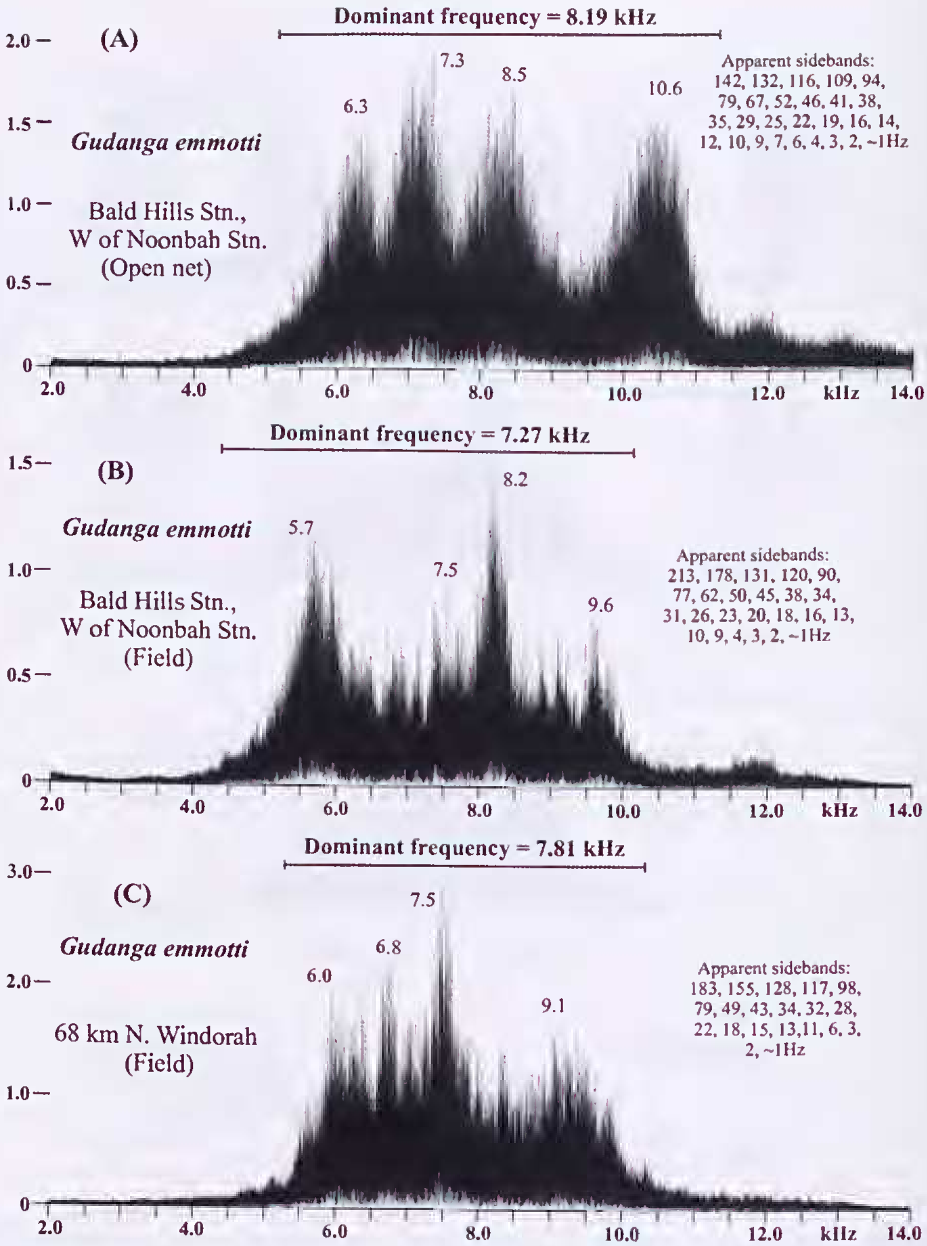


FIG. 17. Amplitude spectra showing, (A) to (C), the frequency distributions within the calling songs of *G. emmotti* from two separate locations within south west Queensland. The dominant frequency is defined by the mean frequency of the main frequency envelope in each plot, shown by the horizontal lines. The numbers against the various peak concentrations are the maximum frequency (kHz) shown by each peak concentration. Also listed are the apparent sidebands as measured within each spectrum. (A), Recording taken from cicada placed in an open net, in the field, from Bald Hills Station, 200 m west of Green Creek, 30.i.2009, south west Queensland. (B), (C), Field recordings, respectively, taken at Bald Hills Station, 200 m west of Green Creek, 30.i.2009, D. Marshall, and 68 km north of Windorah, 1.ii.2009, D. Marshall. Each recording filtered to 2 kHz. The vertical scales are linear relative amplitude scales.

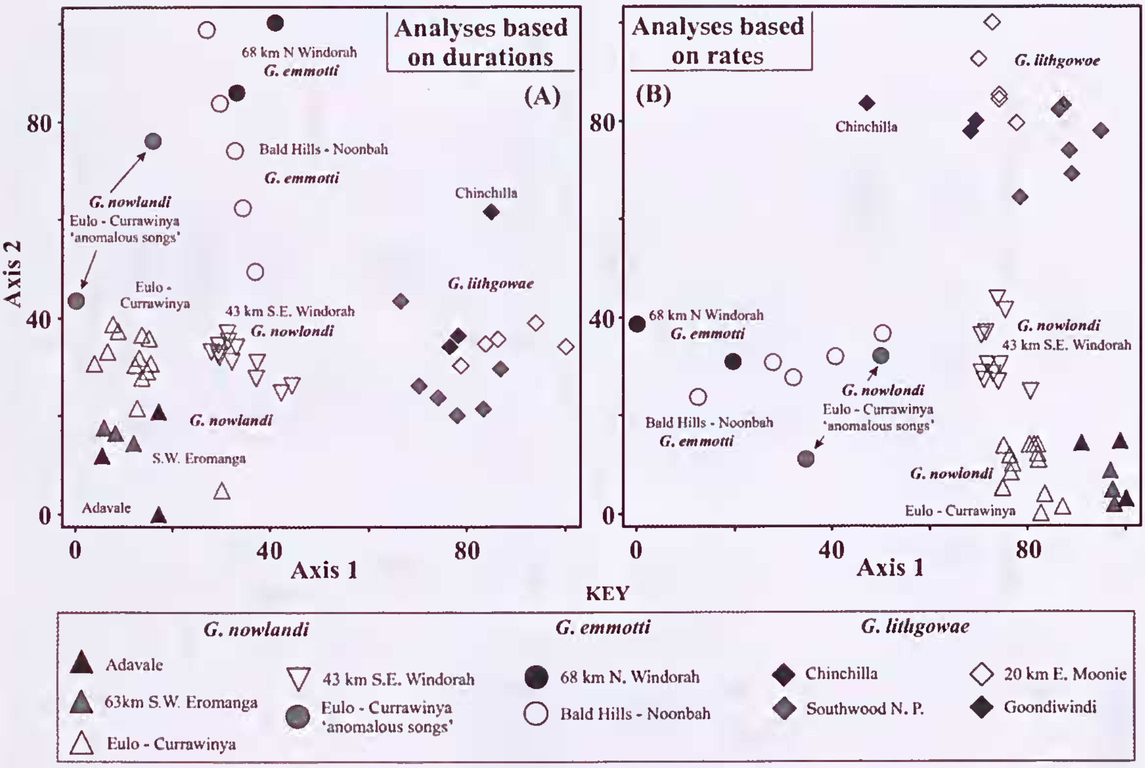


FIG. 18. Results of non-metric multidimensional scaling (NMDS), projected in two dimensions, of the chirping songs of *G. lithgowae, G. nowlandi and G. emmotti*. (A) Analyses based on durations data; (B) based on repetition rates data (see text for details). The results distinguish the three species, and the main population groupings within each species. The two divergent results identified within *G. nowlandi* songs, both from Eulo-Currawinya area, are discussed in the text.

considered to be robust (Faith et al. 1987). Both clustering and ordination procedures were performed on the distance matrix. Cluster analyses (not shown) employed a flexible beta algorithm (ß=-0.25), which is known to exhibit low chaining (Legendre and Legendre 1998). Non-metric multidimensional scaling (NMDS) was conducted on both data subsets. Preliminary runs were performed using four axes, followed thereafter by runs with reduced dimensionality. A scree plot, comparing relative stress vs number of dimensions, and a Shepard plot, showing distance versus dissimilarity, were both used to evaluate the desirable number of dimensions. Stress reduced to acceptable levels (<15%) at two dimensions, so the NMDS ordination procedure was rerun with two dimensions. The ordination of recording instances was then plotted with the original species assignments and groupings identified overlaid onto the plot. These NMDS plots (Fig. 18) provide clearly visible measures of relative similarity between the sets of data. The cluster plots, which are not illustrated, showed very similar patterns of discrimination as those seen in the NMDS plots. The analyses are specifically applied to the chirping phrases, common to each of the three species, and do not incorporate the extended 'buzz' echemes which are effectively confined to *G. nowlandi*.

Kruskal-Wallis analyses and boxplots were used to evaluate differences in specific song parameters between the three-echeme producing species of *Gudanga*. Both of these approaches were chosen because they accom-

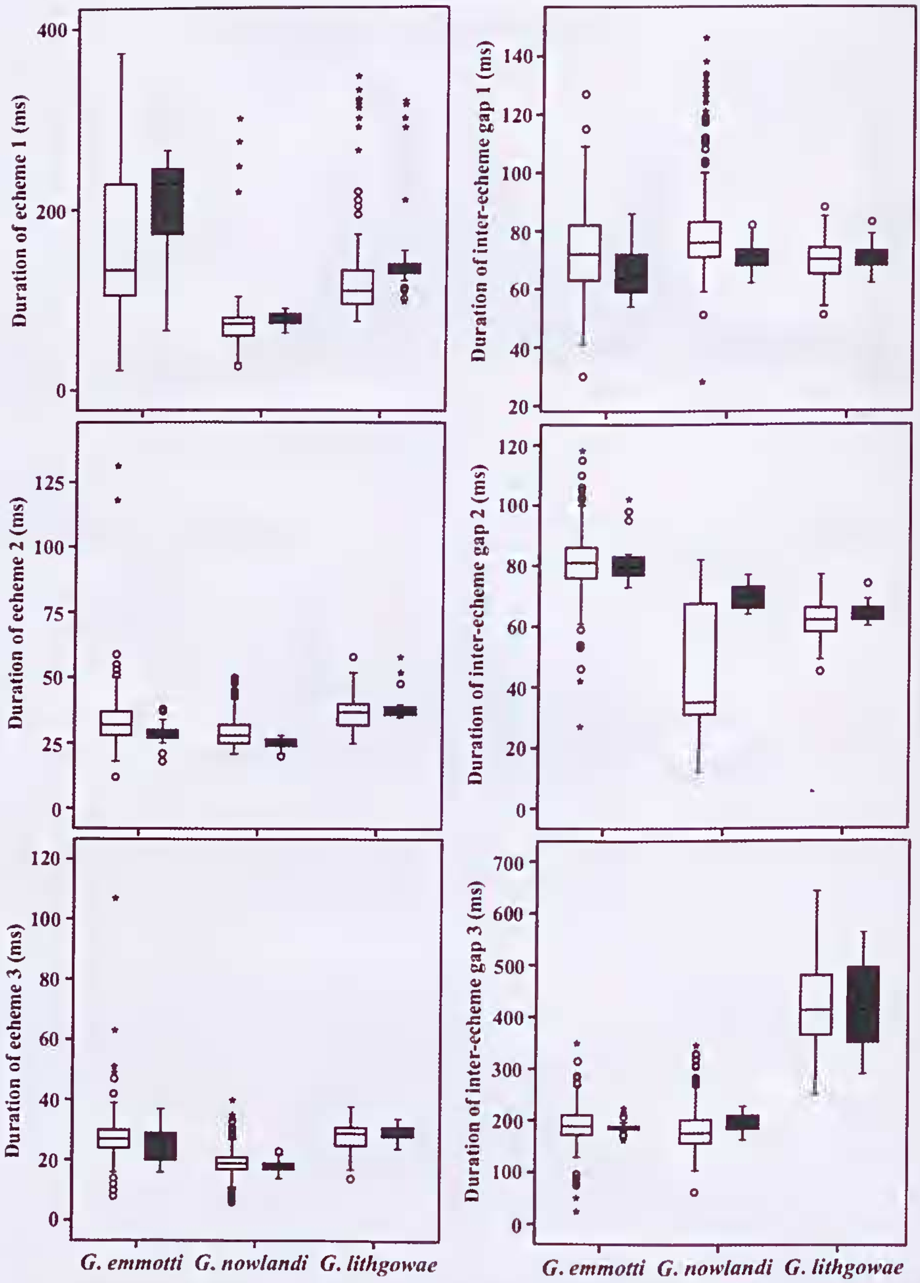


FIG. 19. Boxplots comparing the properties of six song parameters based on durations of the stated parameters for *G. nowlandi*, *G. emmotti*, and *G lithgowae*. The horizontal bars represent median values and the boxes themselves represent the interquartile range (50% of the distribution of the data). The extended bars cover 75% of the distribution of the data, with the circles being outliers that project between 0.5-3 box lengths from either side of the box. Asterisks represent extreme values (>3 box lengths from either side of the box). The boxes without shading are those representing analyses of the total raw data (as in the NMDS analyses). The shaded boxes represent specifically the data for which the male phrases were followed by female wing-flicks.

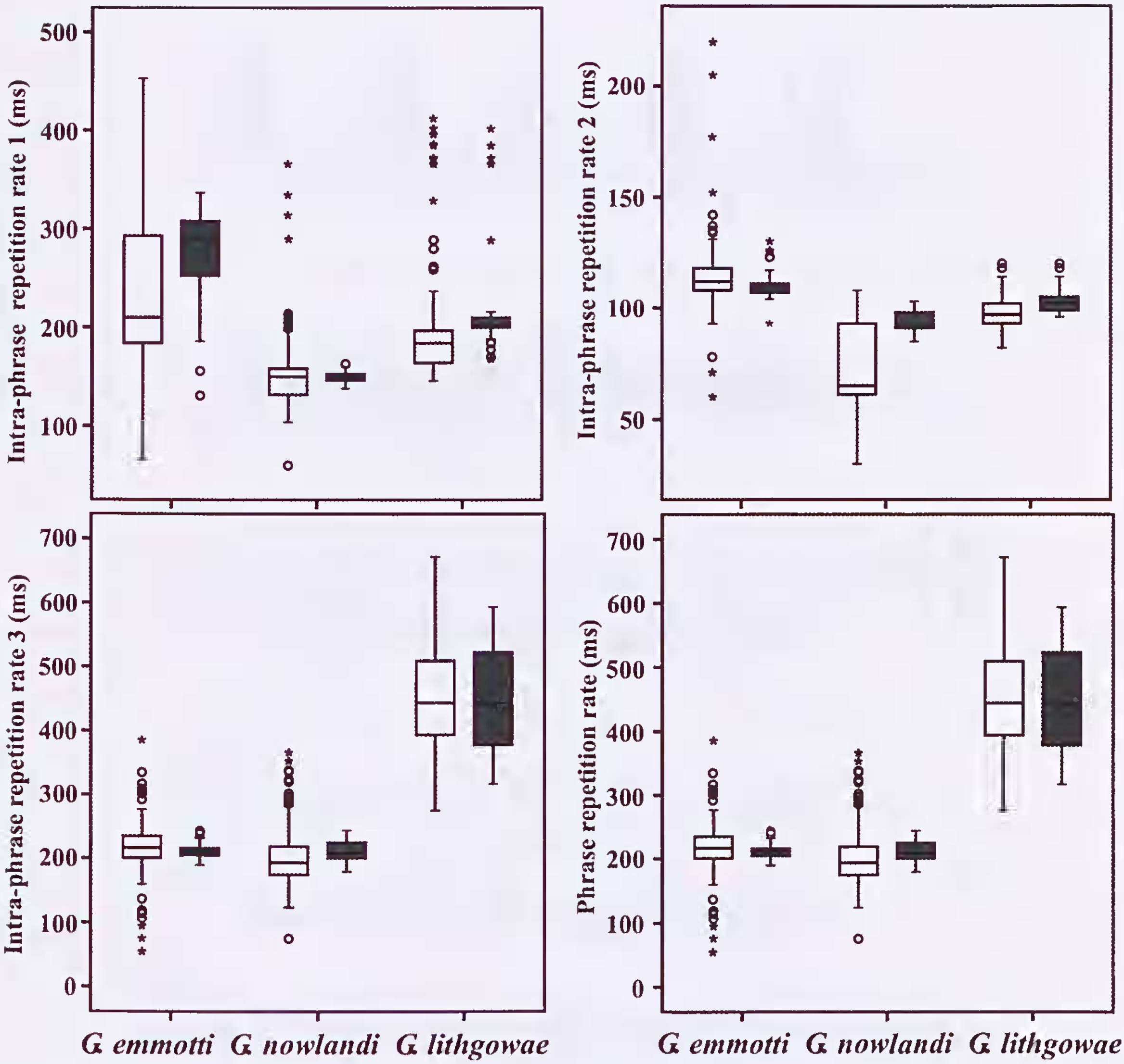


FIG. 20. Boxplots comparing the properties of four song parameters based on repetition rates for *G. nowlandi*, *G. emmotti*, and *G lithgowae*. Symbols and shading as in Fig. 19 caption.

modate the non-linear distributions within the song data. Raw song parameter measurements were sourced from all available recordings from each of the three species of *Gudanga* (rather than averages of recording instances, as used in the NMDS analyses; n=318 for *G. emmotti*, n=609 for *G. nowlandi*, and n=126 for *G. lithgowae*). Phrases that elicit female response flicks were analyzed and plotted separately for comparison, based upon the same parameters described above (Fig. 8) (n=26 for *G. emmotti*, n=31 for *G. nowlandi*, and n=34 for *G. lithgowae*). It is important to note that these represent recordings were made from single localities only (the only such data available).

Results. (Figs 18 to 20, Tables 3, 4). The results show that the songs of the three species are separated on both the NMDS plots, one based on duration data, the other based on rate data.

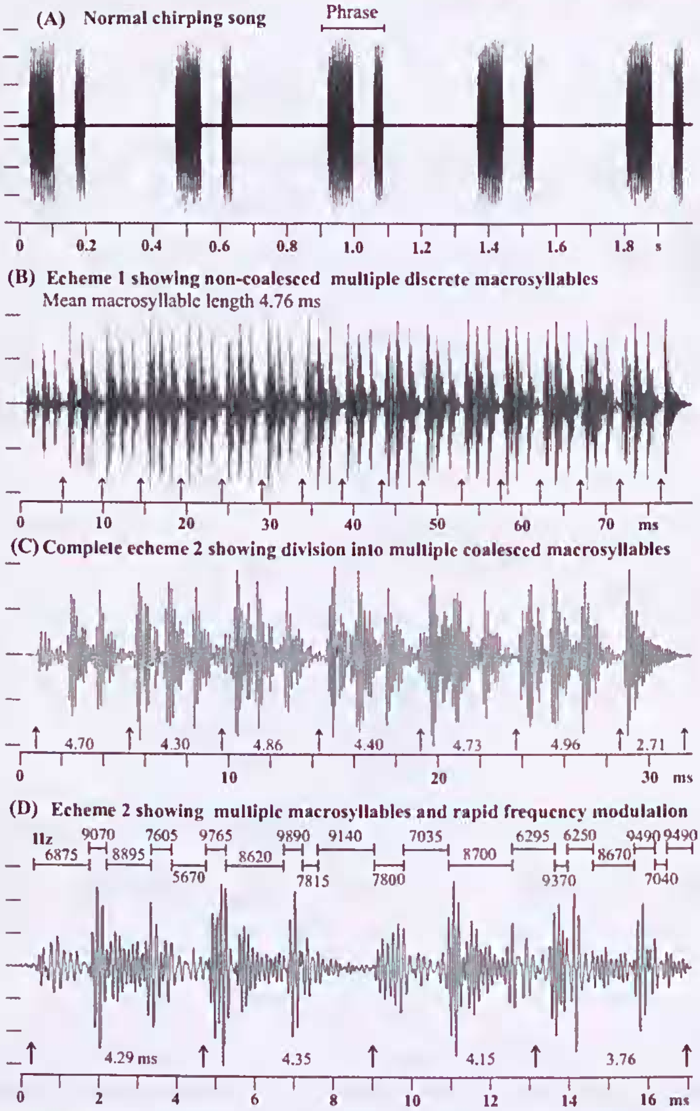


FIG. 21. (Left) *Gudanga adamsi*. Waveform plots showing, (A) gross structure of chirp phrases, each consisting of two echemes with the initial echeme being of longer duration, (B) time expanded detail of a selected complete echeme 1, showing the macrosyllable and syllable structures, the final part of the echeme consists of a single, exponentially decaying syllable of relatively longer duration; (C) a selected single complete echeme 2 showing the individual macrosyllable and syllable structures. Each macrosyllable comprises three syllables, the final segment of the echeme again appears to comprise an exponentially decaying single syllable of greater than normal duration; (D) higher resolution time expansion of segment of an echeme 2 showing greater detail of the syllable structures. The frequencies, measured within the plots from within the different syllable segments, are shown above the waveform. The upward pointing arrows in B to D, show the inferred macrosyllable limits, each of which comprise three (more rarely four) syllables; macrosyllable durations are indicated in ms. (A) to (C), field recordings, filtered to 1 kHz, from the base of the Blackdown Tableland, along Charlevue Creek in eastern-central Queensland, recorded on 17.xii.1985; (D), field recording, filtered (IIR) to 3 kHz, south of Wysby road junction (91.7 km north of Injune), central Queensland, 29.xii.2008, recorded by D. Marshall.

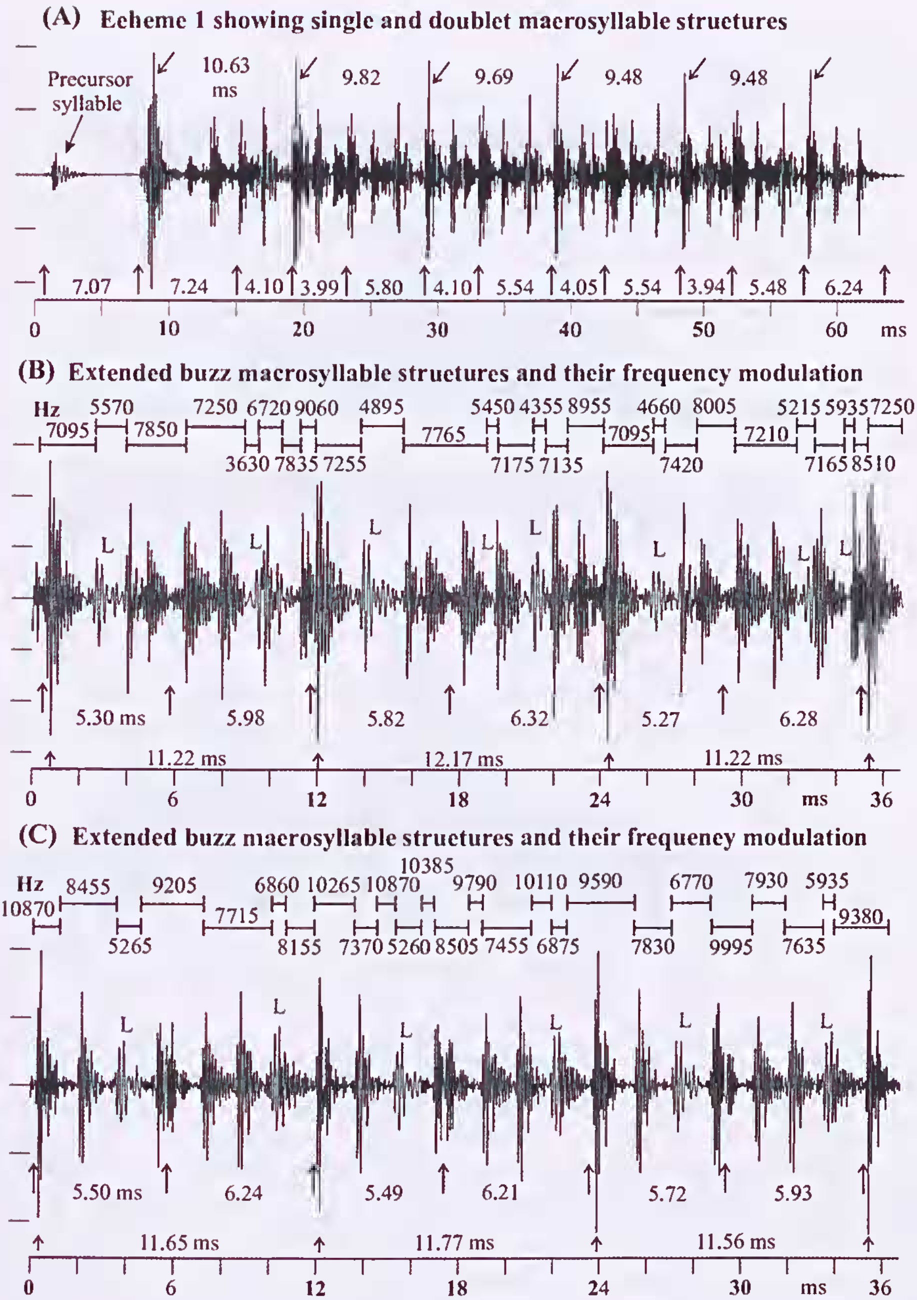


FIG. 22. (Above left) *Gudanga pterolongata*. Waveform plots of (A), (B), the chirping and interspersed extended 'buzz' echeme' phrases. (A) exhibits two extended echemes, (B) a single extended echeme, in both cases followed by short chirp echemes, usually two in number, but varying between one and three; (C) time expanded plot showing more detail of the syllable and inferred macrosyllable structures (macrosyllable limits shown by vertical arrows), including the low amplitude precursor syllable preceding each echeme. Field recordings, filtered to 1 kHz, from 41 km E of Croydon, northern Queensland, taken on 27.i.2005.

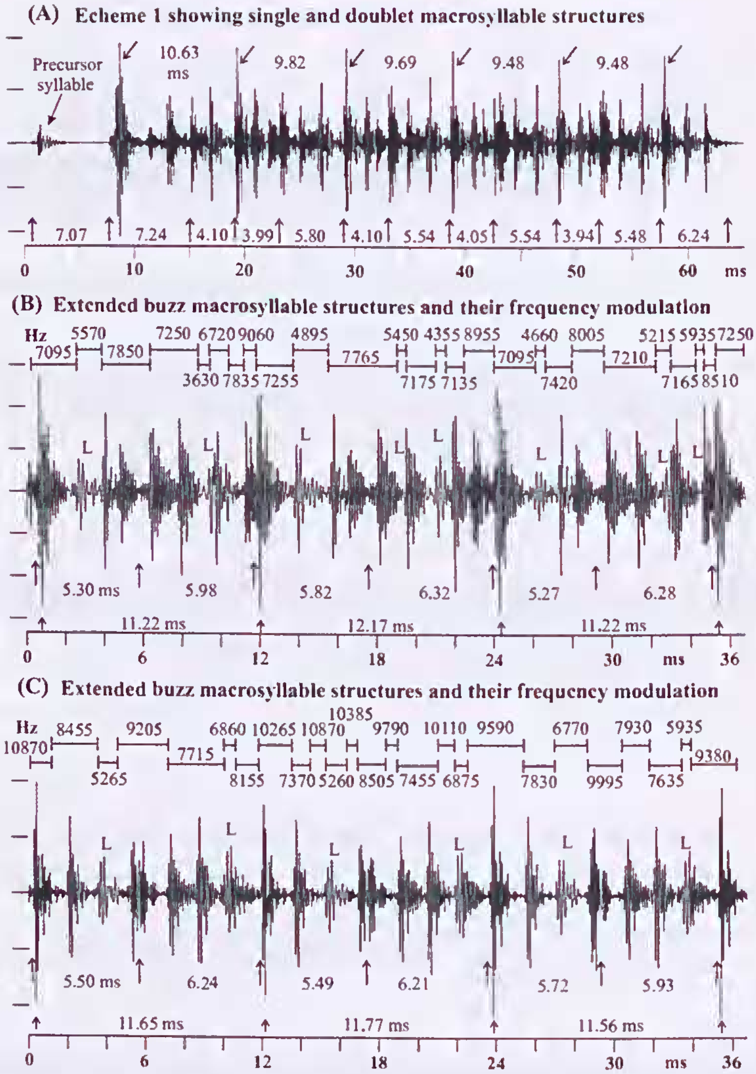


FIG. 23. (Above right) *Gudanga pterolongata*. Waveform plots of; (A), time expansion showing details, from the start of an echeme 1, of syllable and macrosyllable structures, including the precursor syllable and the strongly developed syllable marking the beginning of the echeme. The inclined arrows mark the higher amplitude pulses repeating at 9.5-10.6 ms intervals. These are inferred to define sets of coalesced macrosyllable doublets, the limits of each single macrosyllable indicated by the vertical arrows; number between each vertical arrow are durations in ms. Four syllables occur within each single macrosyllable. (B), (C), further time expanded waveform plots of macrosyllable and syllable structures within extended echemes from separate localities, four (to five) syllables comprising each macrosyllable. The frequencies measured within these plots between and within the syllables are shown above each waveform. The inferred single and doublet macrosyllable limits (and lengths in ms) are indicated by the upper set of vertical arrows. The short segments of lower frequencies are emphasised by the letter 'L', there being one such lower frequency syllable within each macrosyllable, usually the second or third syllable within each. The doublet macrosyllable limits, marked by the higher amplitude pulses, are shown by the lower set of short vertical arrows, noting that these doublet macrosyllable durations are slightly longer than those within the chirp echemes. Field recordings, (A, B), 41 km east of Croydon, northern Queensland, 27.i.2005, unfiltered; (C) 60 km east of Croydon, 30.i.2002, filtered to 2 kHz.

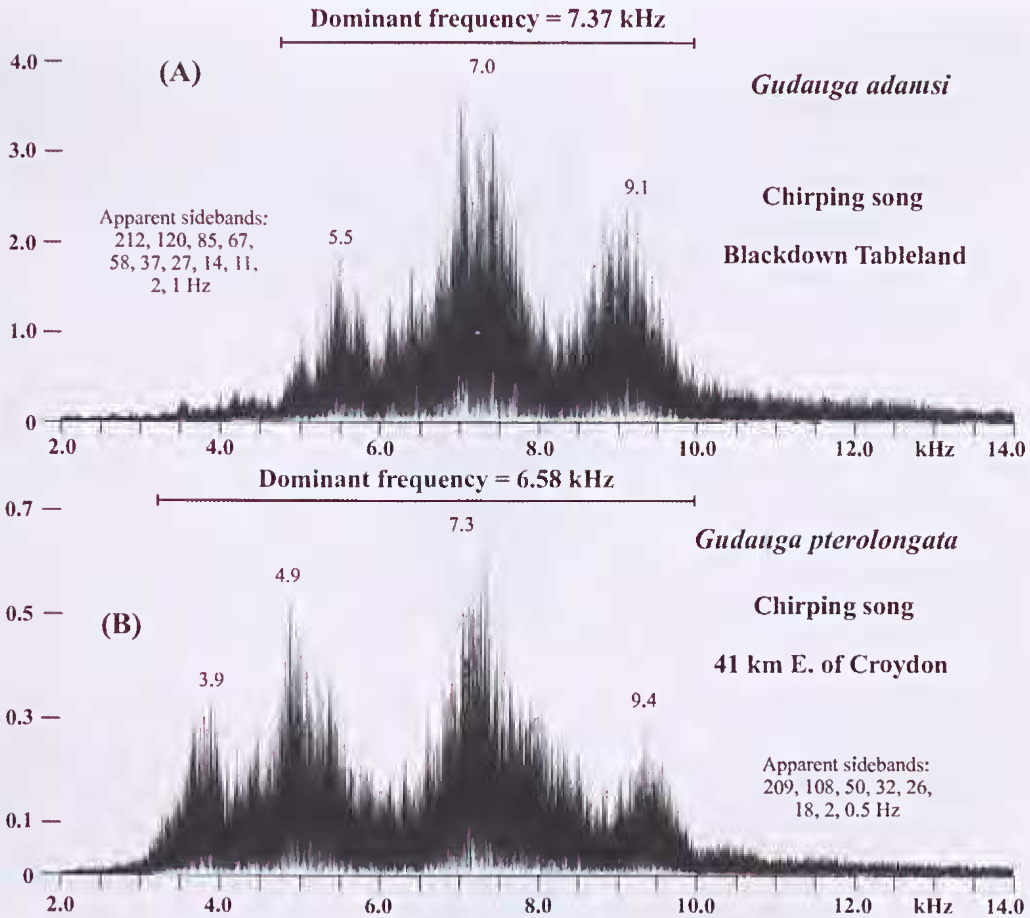


FIG. 24. Amplitude spectra showing the frequency distributions of the calling songs of *G. adamsi* and *G. pterolongata*. The dominant frequency is defined by the mean frequency of the main frequency envelope in each plot, shown by the horizontal lines. The numbers shown against the various peak concentrations within the dominant frequency envelope are the maximum frequency (kHz) shown by each of the peaks. Also listed are the apparent sidebands as measured within each spectrum. Field recordings from, (A), base of Blackdown Tableland, along Charlevue Creek, 27.xii.1985; (B), 41 km east of Croydon, northern Queensland, 27.i.2005. The vertical scales are linear relative amplitude scales.

These plots therefore provide support for the specificity of the calling songs of each of the three species considered, with two cases of partial misclassification within the *G. nowlandi* songs discussed below. Secondly, results point to subtle differences in song properties between regional population groupings, most notable in those of *G. nowlandi*. These populations represent those from ~43 km southeast of Windorah; from the Adavale region; the Eulo-Currawinya region; and ~63 km southwest of Eromanga, this latter data set not strongly separated from the Adavale populations although geographically well separated (Fig. 7).

The case of the *G. nowlandi* population ~43 km southeast of Windorah is significant in at least two ways. First, the distinct separation of its song parameters from the other studied *G. nowlandi* populations, and secondly, the closer proximity of its song vectors in the NMDS plots to those of *G. emmotti* (Fig. 18). This population is, in fact, the closest geographically to the known areas of *G. emmotti* distribution

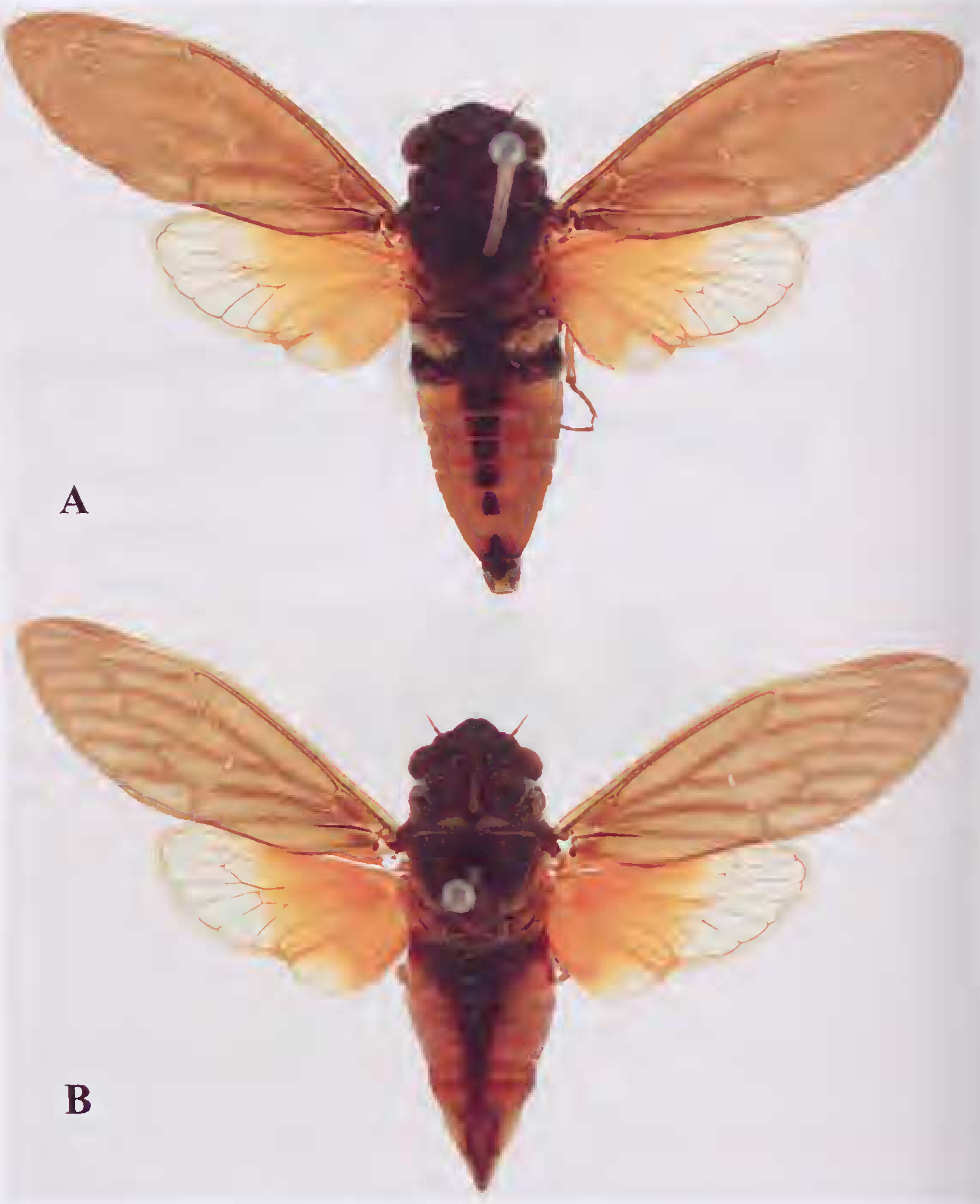


Plate 1. *Gudanga lithgowae*. A. male, from Warrego-Auburn Road junction, Chinchilla, southeast Queensland, body length 15.6 mm. B. female, from same locality, body length 18.5 mm.

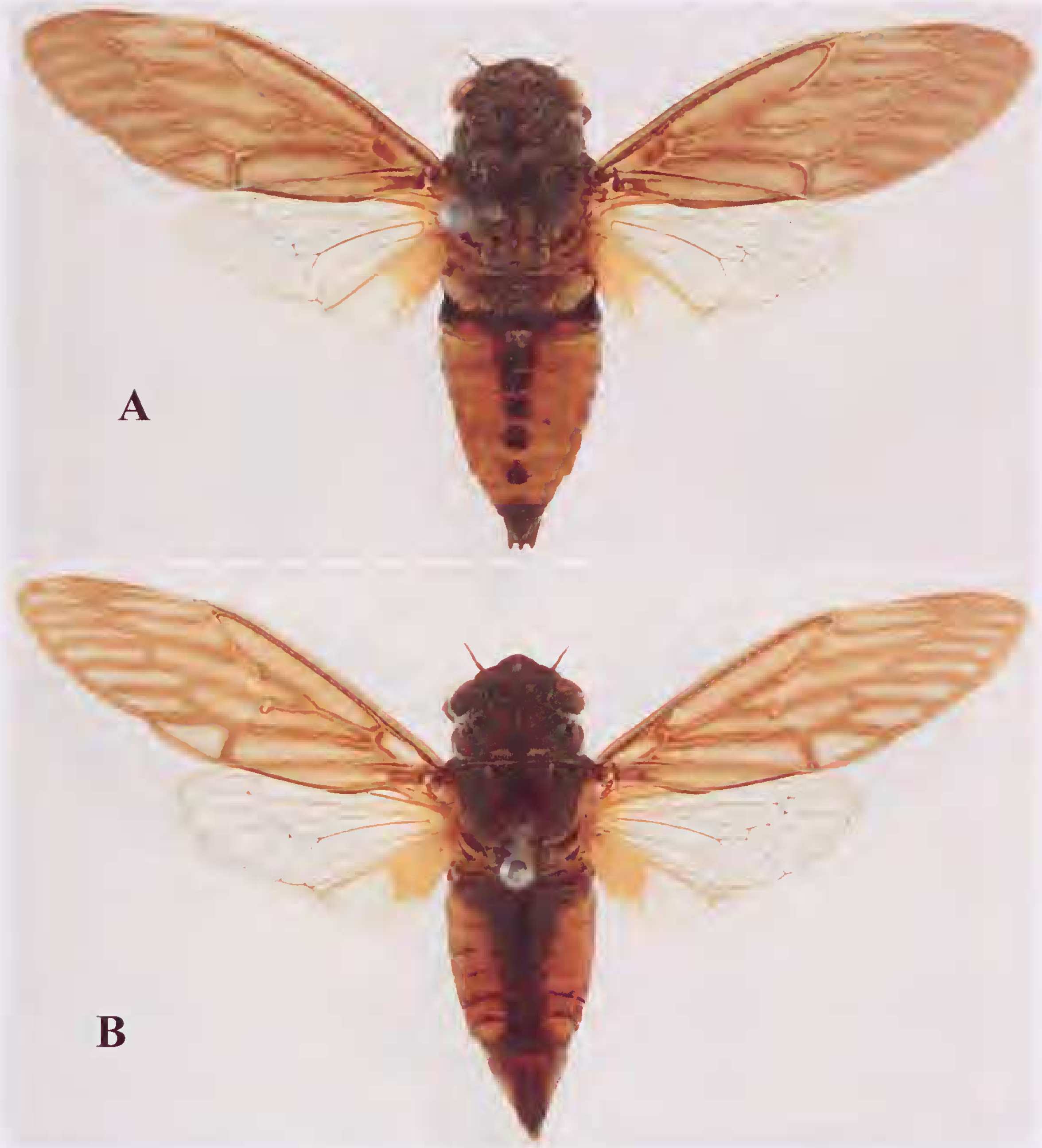


Plate 2. *Gudanga nowlandi*. A. male, 'Bulls Gully H.S.', lagoon, Adavale, southwest Queensland, body length 17.3 mm. B. female, 17 km northeast of ' Milroy H.S.', near Adavale, southwest Queensland, body length 18.5 mm.

Plate 3. *Gudanga emmotti*. A. male from 200 m west of Green Creek, Bald Hills Station, southwest Queensland, body length 18.1 mm. B. female, from 68 km north of Windorah, southwest Queensland, body length 18.5 mm.

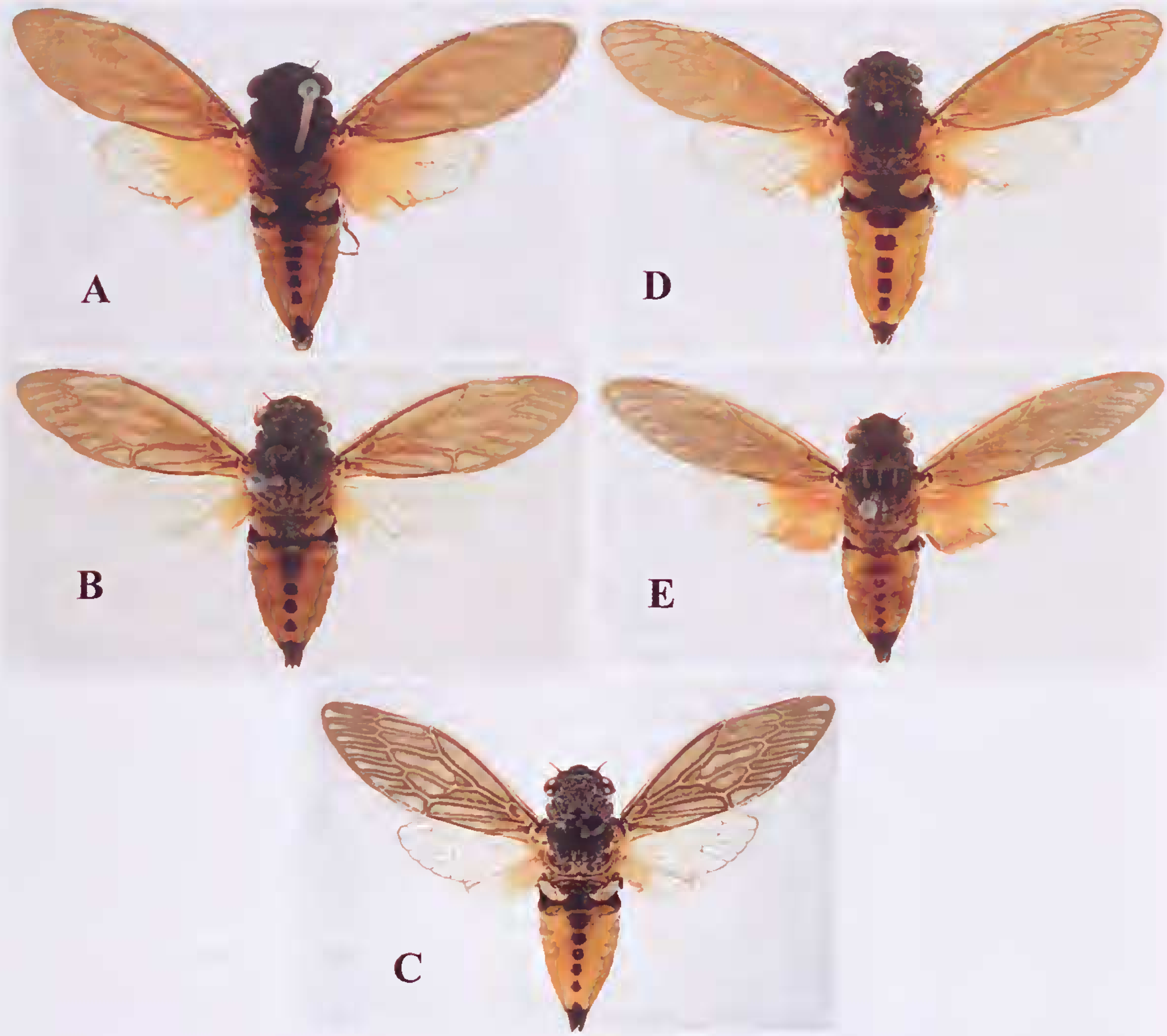


Plate 4. Comparison of males of: A, *Gudanga lithgowae*, details as in Plate 1 caption. B. *Gudanga nowlandi*, details as in Plate 2 caption. C. *Gudanga emmotti*, details as in Plate 3 caption. D. *Gudanga adamsi*, base of Blackdown Tableland, Charlevue Creek, east-central Queensland, body length 16.6 mm. E. *Gudanga pterolongata*, 60 km east of Croydon, Georgetown Road, north Queensland, body length 18.3 mm.

(Fig. 7) and therefore suggestive of possible introgression between the two species within this population. However, morphological characters in this population, including pygofer morphology (single specimen only; see taxonomy above) were found to be consistent with *G. nowlandi*.

The two cases of *G. nowlandi* partial misclassification require explanation, both examples occurring in cicadas in relatively close geographical proximity within the Eulo-Currawinya region, specifically 29.5 and 31.8 km south of Eulo (fifteen separate insects recorded from the general locality). The data in one case diverge markedly away from typical *G. nowlandi*, and project towards the *G. emmotti* vector fields in both NMDS plots. This case occurs in a single recording in which a number of atypically long echeme 1's are embedded within otherwise normal sets of phrases and phrase lengths (shown in full in Fig. 13A; see also Fig. 11), though apparently influencing the mean duration of echeme 1. This recording, however, also exhibits multiple instances of extended 'buzz' echemes characteristic of *G. nowlandi*, including one at the commencement of the 'atypical' segment. Overall, apart from the anomalies involving some extended variations of echeme 1, the recorded song matches recordings typical of *G. nowlandi*.

The second anomalous case has resulted in the projected song data diverging from the *G. nowlandi* fields, although not projecting especially close to the *G. emmotti* field, most clearly seen in Fig. 18B. The anomalous characters within this song occur throughout a single recording (38s duration), of a single insect. All other recordings from this same locality show no similar anomaly. The anomaly results from subtle but consistently elevated inter-echeme 1 to 2 repetition rates and inter-echeme 1 to 2 intervals, which further result in similarly elevated phrase repetition rates (documented in Table 3). Within the plot of the echeme 1 durations versus phrase repetition rates (Fig. 11), the 'anomalous' data set represented in this recording clearly plot within the *G. nowlandi* song field. Additional evidence that this recording is that of *G. nowlandi* is provided again by the presence of the characteristic, multiple extended 'buzz' echemes in the recording. Although isolated 'anomalous' song parameters do occur in many recordings of individual cicadas (as shown by the minimum-maximum parameter limits shown in Table 3), the 'atypical' parameters described previously differed in being persistent throughout the recording in question.

The statistical results illustrate several aspects of the song properties of these three very similar species: (i) The chirping songs are, with the two previously noted *G. nowlandi* anomalies from the Eulo-Currawinya region, clearly separated by the statistical methodology used, based on the duration and rate song parameters. The emission of extended 'buzz' echemes in many *G. nowlandi* songs is an additional characteristic parameter that refines the recognition of the songs of this species, specifically removing the uncertainty of the two 'atypical' cases discussed. The recordings of multiple songs at these localities in particular suggests that as more song data are collected, inevitably more 'atypical' song parameters will be encountered. (ii) Inherent calling song variability between the main *G. nowlandi* populations sampled is shown by the cluster and NMDS plots, by the compiled data for each population (Table 1), and even by simple echeme 1 duration comparisons (Fig. 10B, 11B), all indicating song parameter shifts within the different regional populations. The songs of the populations from Adavale and the Eulo-Currawinya areas are relatively similar in both NMDS plots. The songs of the population from 63 km southwest of Eromanga are very similar to the Adavale songs, notwithstanding the significant geographic separation involved. It is the population from 43 km southeast of Windorah that is the most divergent, as previously noted, perhaps indicative of more persistent isolation. This area lies near the eastern limit of the Simpson sand dune systems and is certainly relatively arid, probably more so than the other areas from which the *G. nowlandi* populations were sampled. (iii) The statistical results also highlight some systematic song variability within and between populations of both *G. emmotti* and *G. lithgowae*. Although not sufficient to break down the specificity of the calling songs, such variability does appear to be characteristic of southern Queensland *Gudanga* songs, presumably a key to their song evolution.

Boxplots (Figs 19, 20), based on statistical comparisons (Table 4) of the total raw song parameter measures reveal a number of differences between the three *Gudanga* species with the three-echeme song type. Differences, at high levels of significance, are seen across most of the parameters (Kruskal-Wallis, $p<0.01$) between the three species, as also illustrated in the boxplots. Exceptions are noted in the inter-echeme gap 1 data between *G. emmotti* and *G. lithgowae* ($p>0.05$). The statistically strongest differences that are evident between the three species are the echeme durations, the inter-echeme gaps 2 and 3, the phrase repetition rates and each of the intra-phrase repetition rates, the distribution of which can be seen in the respective boxplots.

The statistical results again show that the differences between the three species based on song phrases followed by female wing-flicks are similarly highly significant ($p<0.01$), important as these parameters are specifically recognised by the females. The least significant parameters are the inter-echeme gap 3 and intra-phrase repetition rate 3 ($p>0.19$) between *G. emmotti* and *G. nowlandi*, and the inter-echeme gap 1 ($p>0.27$) between *G. nowlandi* and *G. lithgowae*. These statistical analyses again emphasise the importance of song recognition in differentiating these morphologically very similar three species. An additional aspect is the comparison of individual parameters between the total raw data and the data in which song phrases are followed by female wing-flicks. The box plots suggest that for most parameters, there is significant overlap. Differences are more readily apparent when independent song parameters are treated in combination (Fig. 18). A notable exception, seen in the *G. nowlandi* data, are those of inter-echeme gap 2 and the partially interdependent intra-phrase repetition rate 2, which are revealed to be quite distinct in duration (Figs 19, 20).

The Two-Echeme Song Types.

The chirping calling song phrases of *G. adamsi* and *G. pterolongata* consist of two echemes, the initial echeme (echeme 1) longer in duration than the following echeme (echeme 2; Figs 8A, 21 to 24; Table 2). Extended 'buzz' echeme phrases are also commonly emitted by *G. pterolongata*, between 0.65-5.5 seconds in duration, interspersed within the normal chirp phrases (Figs 22A, B; Table 2), similar to those emitted by *G. nowlandi*. These extended 'buzz' echemes are not always emitted, being most commonly emitted when the cicada populations are relatively high. The timing of insertion of these extended echemes into the chirping song occurs in three different ways; (a) between the two echemes within a single chirp phrase, in some cases with coalescence of echeme 1 into the start of the following extended echeme (the second extended echeme in Fig. 22A). (b), insertion between separate chirp phrases (Fig. 22B), in which case they are followed by sets of two, rarely three short echemes; and (c) emitted at the end of a long series of chirping phrases, thereby terminating a given song sequence. There is no evidence of any systematic changes of echeme durations, inter-echeme intervals or intra-echeme repetition rates immediately preceding or following extended echeme emission. Extended 'buzz' echemes have not been recorded within the *G. adamsi* calling songs.

The chirping songs are described by five temporal parameters (Table 2; Fig. 8). Comparison of these between *G. adamsi* and *G. pterolongata* show extensive overlap, the echeme 2 durations tending to be slightly longer in *G. pterolongata*. The extended echemes and finer scale macrosyllable structures (see below) distinguish the *G. pterolongata* songs.

The chirping songs of *G. adamsi* exhibit similar temporal properties in the various localities for which song recordings have been made, with the exception of the localities 30-35 km south of Blackwater. Here, a subtle but consistent reduction is recognised in the echeme 1 durations compared to all other locations sampled, as documented in Table 2. These are not accompanied by readily discernable morphological or colour differences. Research in progress sequencing mitochondrial DNA within Australian cicadas, including the *Gudanga* species, has identified a distinctive genetic divergence within this particular *G. adamsi* population (K. Hill, pers. comm.).

Fine-scale macrosyllable structures. The chirp and extended 'buzz' echemes comprise multiple discrete macrosyllables which typically vary in their degree of coalescence. Figs 21B-D illustrate examples of discrete macrosyllables within echemes 1 and 2 of *G. adamsi*. Each macrosyllable, the mean lengths of which are 4.5 ms (Table 2), comprises three syllables. The terminating syllable within the echemes is characterised as a single exponentially decaying syllable, longer than the remaining syllable durations within the echemes, although shorter than the macrosyllable lengths (Fig. 21C). A comparable feature is seen within the terminations of echemes within the *G. lithgowae* songs. When viewed in more detail in time expanded waveform plots (Figs 21D), measured frequencies of the syllables and pulses within the macrosyllables of the *G. adamsi* song show very rapid and sharply defined modulations, both between and within syllables. The highest amplitude groups of pulses typically mark the initiation of most syllables, and are characterised by relatively elevated frequencies, usually >9 kHz. The wide range of measured frequencies measured in these detailed waveform plots is consistent with the broad frequency range limits shown by the amplitude spectrum (Fig. 24A).

The detailed structures of the chirp and extended echemes within the *G. pterolongata* songs differ from those of *G. adamsi*. One clearly defined feature is the presence of an exponentially decaying precursor syllable, followed after an interval of some 7-7.5 ms, by the initial syllable of the echeme itself (Figs 22C, 23A). This initial echeme syllable is itself distinctive, being sharply defined, with higher amplitude and slightly longer duration than the following syllables comprising the macrosyllable sequences (Fig. 23A). A conspicuous character of the macrosyllable structures within this species is their regular repetition, marked by single high amplitude pulses, with repeat intervals of near 10 ms (9.1-12.2 ms), i.e. ~100 Hz (Figs. 23A-C; Table 2). Each of these 10 ms segments, on detailed examination, is seen to represent coalesced double macrosyllables, each macrosyllable comprising four to five syllables. These exhibit rapid and marked frequency modulations in which the second or third syllable are of lower frequency. The final syllable of each macrosyllable is typically of relatively higher frequency (≥9 kHz), as illustrated in Figs 23B, C. The range of frequencies measured in the waveform plots are consistent with the amplitude spectrum determined from a larger sampling of the song (Fig. 24B).

Amplitude spectra. (Figs 24A, B) The spectra of the calling songs of *G. adamsi* and *G. pterolongata* are comparable to those previously described for the three-echeme song types. They again exhibit very broad band frequencies, also evident in the above described time expanded waveform plots. The dominant frequencies exhibit similar ranges and magnitudes as observed for the songs of *G. lithgowae, G. emmotti and G. nowlandi*. A crude periodicity is present within the *G. adamsi* and *G. pterolongata* spectra of the individual peaks within the dominant frequency envelopes, on scales of ~1.5-2 kHz, possibly reflecting very fine scale syllable structures. The complex sideband ranges must reflect the complexities inherent in the syllable, macrosyllable, echeme and phrase structures of the calling songs, those in the ~100 Hz range in the *G. pterolongata* songs probably correlating with the doublet, repetitive macrosyllables.

Distribution (Fig. 7). ***Gudanga adamsi***. (Figs 1D-6D; Pl. 4D). Additional localities to those listed in Moulds (1996) include brigalow woodland in the north eastern corner of the Isla Gorge National Park (25° 10.02′S 150° 00.73′E), AE; the Brigalow Research Station, approximately 30 km northwest of Theodore (24°48.85′S 149°47.48′E), AE, LWP; the boggomoss site near Glebe Weir, Dawson River, north east of Taroom, ~ 25° 28′S 150° 02′E, QM; 31 km south of Blackwater (23° 52.14′S 148° 53.65′E), MSM; 44.4 km south of Rolleston (24° 50.28′S 148° 31.81′E); 91.7 km north of Injune (25° 08.14′S 148° 34.95′E), MSM; Little Windeyer Creek crossing, 28 km north of Tambo (24° 40.19′S 146° 22.19′E), MSM; Lonesome National Park, 47 km northeast of Injune, 25° 29.40′S 148° 49.92′E, QM reference numbers T189497, 8, 9, QM. These localities are all in central and eastern central Queensland.

G. pterolongata (Figs 1E-6E, Pl. 4E). This species has been observed in extensive lancewood (*Acacia shirleyi*) forest areas, extending from 23 km E of Croydon, eastwards to near, and probably just east of the Gilbert River crossing, approximately 70 east of Croydon, adjacent to the Croydon-Georgetown road, north Queensland. It occurs in both disturbed and undisturbed lancewood forest, which occur along the top of laterite plateau (the western margin of which is 23 km E. Croydon), but is apparently absent from mixed woodland with only minor lancewood presence. Distributional data presented by Beadle (1981, p. 461) for lancewood woodlands in this region indicate that they extend in a broad band for approximately 200 km northwest of the Croydon-Gilbert River localities, and in a narrow belt south-eastwards for a comparable distance. It is therefore anticipated that the distribution of *G. pterolongata* will at least partially follow these broader regional lancewood occurrences, depending on appropriate soil and climatic conditions.

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